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Chitinozoan biozonation in the upper Katian and Hirnantian of the Welsh Basin, UK

T.J. Challands [a,*], T.R.A. Vandenbroucke [b,c], H.A. Armstrong [d], J.R. Davies [e]

[a] School of Geosciences, Grant Institute, University of Edinburgh, West Mains Road, Kings Buildings, Edinburgh EH9 3JW, UK
[b] Géosystèmes, UMR 8217 CNRS, Université de Lille 1, SN5, Cité Scientifique, 59655 Villeneuve d'Ascq, France
[c] Palaeontology, Department of Geology, Ghent University, Krijgslaan 281/S8, 9000 Ghent, Belgium
[d] Department of Earth Sciences, Durham University, Science Labs, Durham DH1 3LE, UK
[e] Department of Geography and Earth Sciences, Aberystwyth University, Aberystwyth SY23 3DB, UK

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A B S T R A C T

Here we present a chitinozoan biostratigraphical framework for the South Wales upper Katian and Hirnantian (Ashgill) succession. The current study indicates that three of the six Avalonian Ashgill chitinozoan biozones are recognised in the Welsh Basin; the *bergstroemi*, *fossensis and umbilicata* biozones. The Baltoscandian and Laurentian *Hercochitina gamachiana* biozone is suggested by the presence of *Belonechitina* cf. *gamachiana* and the *Spinachitina taugourdeaui* biozone is suggested by *Spinachitina* cf. *taugourdeaui*. Intervening between these is a newly erected lower Hirnantian regional biozone, the *Belonechitina llangrannogensis* n. sp. biozone. The late Katian (Cautleyan–Rawtheyan) *Conochitina rugata* biozone was not recognised, though the index taxon is recorded. The presence of *B.* cf. *gamachiana* below the lithological expression of the Hirnantian glacial maximum and alongside Rawtheyan graptolite and trilobite assemblages shows that the local base of the *B.* cf. *gamachiana* biozone lies beneath the Katian–Hirnantian boundary. Although at present in open nomenclature, the finds of *B.* cf. *gamachiana* and *S.* cf. *taugourdeaui*, from sites where these chitinozoans co-occur with graptolites, are potentially important; the area offers the potential to study how *B.* cf. *gamachiana* and *S.* cf. *taugourdeaui* are taxonomically and stratigraphically linked to the original index species. A composite Katian–Hirnantian chitinozoan biozonation for the Welsh Basin is presented and three new species are defined: *Belonechitina llangrannogensis* n. sp., *Belonechitina ceregidionensis* n. sp. and *Spinachitina penbryniensis* n. sp.

1. Introduction

The recent development of an integrated Upper Ordovician chitinozoan biozonation in British Avalonia (Vandenbroucke and Vanmeirhaeghe, 2007; Vandenbroucke, 2008a), based on type areas for the British chronostratigraphical scheme (Fortey et al., 1995, 2000), recognises six chitinozoan biozones with two subzones for the upper Katian (Ashgill) and potentially provides a powerful tool for dating Upper Ordovician successions where graptolite preservation is not favourable. However, the applicability of the UK scheme, as it currently stands, has not been widely tested outside the type areas on which it was based and there remain problems concerning calibration with graptolite and conodont-based biostratigraphies as well as other regional and global stratigraphical schemes (Vandenbroucke, 2008a). Significantly, the development of a UK Avalonia chitinozoan biozonation coincided with the recent British Geological Survey (BGS) re-mapping of the Lower Palaeozoic Welsh Basin and its margins that represent the historic type area for the Ordovician and Silurian systems (e.g. Murchison, 1839; Lapworth, 1879). The work reported here links closely with Vandenbroucke et al.'s (2008b) study of Darriwillian (Llanvirn) to mid-Katian (late Caradoc) chitinozoans in the Fishguard–Cardigan area and with work on late Hirnantian and Silurian assemblages in mid-Wales (Vandenbroucke et al., 2008a), from the Type Llandovery succession (Davies et al., 2013) and from Wenlock rocks in the Builth Wells district (Verniers, 1999).

Here we present a regional biostratigraphical scheme that utilises data on chitinozoan abundance and distribution from the well-constrained upper Katian–Hirnantian Welsh Basin succession (Davies et al., 1997, 2009) and compare it to that proposed by Vandenbroucke (2008a). This has allowed the reproducibility of the new British Avalonia chitinozoan biostratigraphical scheme to be tested and, additionally, the influence of sedimentary facies (i.e. basin and shelf) to be assessed.

The chitinozoan biozonation presented herein also informs correlation of the Cardigan Bay succession (Cardigan to Llangrannog) of west Wales (BGS, 2003, 2006; Davies et al., 2003, 2006) with the easterly successions of the Tywi Anticline, Garth and Type Llandovery areas (Schofield et al., 2004; BGS, 2005, 2008; Schofield et al., 2009; Davies et al., 2013) where graptolites are less common and many chronostratigraphic boundaries are poorly constrained. In addition, the mid-southern hemisphere palaeolatitude position of the Welsh Basin during the Late Ordovician

* Corresponding author. Tel.: +44 131 650 8543.
E-mail address: tom.challands@ed.ac.uk (T.J. Challands).

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makes the area important as a stepping stone between latitudinally restricted polar and tropical chitinozoan provinces that are difficult to correlate (Delabroye and Vecoli, 2010; Vandenbroucke et al., 2010; Ghienne et al., in press).

2. Palaeoenvironmental setting and lithostratigraphic framework

The Welsh Basin provides a relatively complete section through Katian (upper Caradoc–lower Ashgill) and Hirnantian (upper Ashgill) rocks formed in turbiditic slope-apron to muddy shelf depositional settings (Davies et al., 1997) (Figs. 1 and 2). The line of demarcation between late Ordovician basinal and shelfal settings was located along the eastern flank of the Tywi Anticline where long-lived fractures, including the Llanwyrtyd and Garth fault systems and the Crychan Fault Belt, were influential in controlling facies distribution (e.g. Davies et al., 1997; Schofield et al., 2004; Davies et al., 2009; Schofield et al., 2009). As elsewhere, the Katian–Hirnantian Welsh Basin succession records the increasing impact of the late Ordovician glaciation including its mid-Hirnantian acme (e.g. Davies et al., 2009 and references therein). The repeated and linked changes in sea level, organic productivity and basin water oxicity that accompanied this event are reflected in marked variations in levels of bioturbation and organic content. This allows burrow-mottled and bioturbated *oxic* facies to be distinguished from typically darker *anoxic* facies in which burrow-mottling is absent, organic content is high and hemipelagic lamination and graptolites are commonly preserved (e.g. Davies et al., 1997; Challands et al., 2009).

The oldest basinal rocks assessed here are from the Cardigan area where the lower–middle Katian (upper Caradoc–?lower Ashgill) Dinas Island Formation includes the distinctive, dark and anoxic Cwm Degwel Mudstone Member (up to 100 m thick) at its top and where there is a lateral passage into the coeval Cwm-yr-Eglwys Mudstone Formation (Davies et al., 2003; Williams et al., 2003). The succeeding middle–upper Katian (lower Ashgill) burrow-mottled Nantmel Mudstones Formation is over 1 km thick along the Cardigan Bay coast where it occupies the cliffs between Cardigan and Penbryn. The formation's extensive inland outcrop ranges eastwards as far as the Llandovery

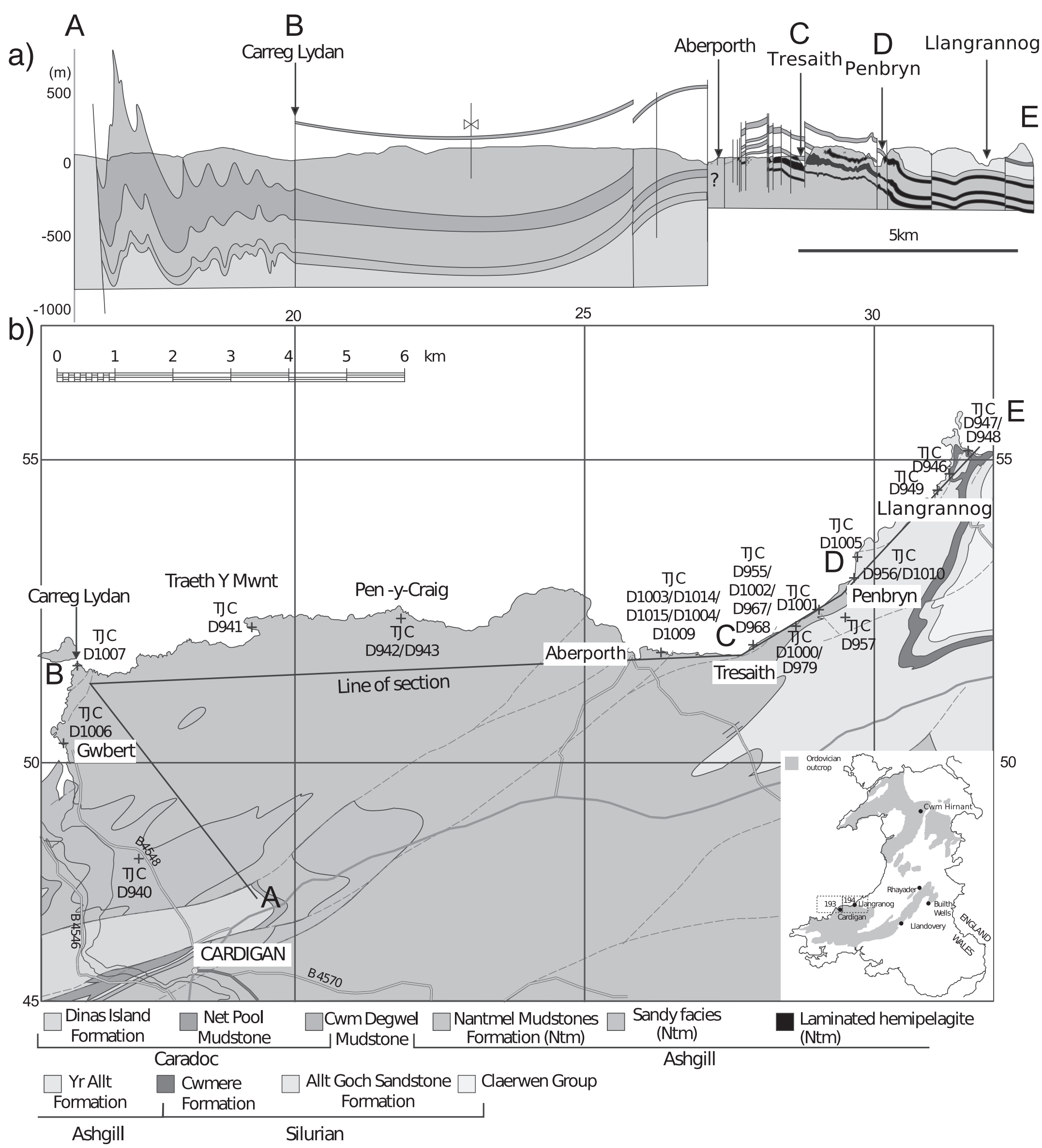

Fig. 1. Middle Katian (upper Caradoc) to lower Silurian geology of the Cardigan Bay area (based in part on BGS, 2003, 2006): a) elevation profile and cross-section along the line shown in b; b) geological map and chitinozoan sample locations. Inset map shows limits of Ordovician outcrop in the Welsh Basin.

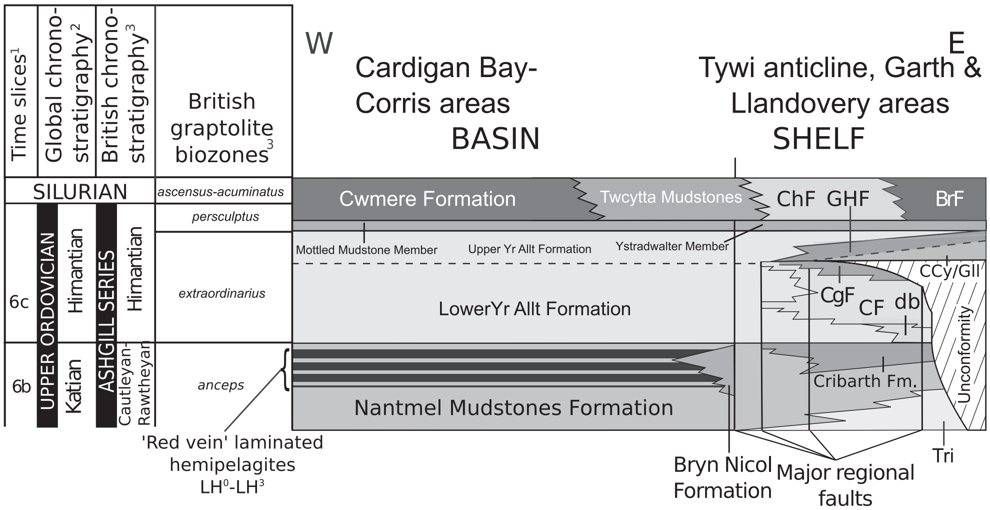

Fig. 2. Section comparing the lithostratigraphy of the Welsh Basin centre (Cardigan Bay–Corris areas) with that of its eastern margin and shelf (Tywi Anticline, Garth and Llandovery areas) (principally after Davies et al., 1997, 2003, 2006; Schofield et al., 2004, 2009) relative to the chronostratigraphal schemes of [1]Webby et al. (2004), [2]Bergström et al. (2006) and [3]Fortey et al. (2000). BrF = Bronydd Formation, CCy = Cwm Clyd Sandstone Foration, CF = Ciliau Formation, CgF = Cwmcringlyn Formation, ChF = Chwefri Formation, db = disturbed beds (of Ciliau Formation), Gll = Glasallt-Fawr Sandstone Formation, LH^0–LH^3 = Laminated hemipelagite units 0–3, Tri = Tridwr Formation.

and Garth areas and its correlatives are seen in the core of the Plynlimon Inlier and in the Corris area (Cave and Hains, 1986; Pratt et al., 1995). Present in the upper part of the Nantmel Mudstones are widely recognised organic-rich, anoxic and graptolitic laminated hemipelagic mudstone units (labelled LH) that together comprise the Red Vein of Pugh's (1923) Corris area succession. Up to four anoxic units have been recorded which Challands (2008) and Challands et al. (2009) number LH^0 (lowest) to LH^3 (highest) (Figs. 1 & 2).

As at the coast, the dominantly oxic Nantmel Mudstones Formation of the Tywi Anticline succeeds an anoxic lower Katian succession that comprises the St. Cynllo's Church Formation and in which an upper, richly graptolitic, mudstone unit (Sugar Loaf Member) has been recognised. The local Red Vein anoxic facies here interleave with the fault-located debrites and shelly turbidites of the Bryn Nicol Formation. Further east, lower levels of the Nantmel Mudstones Formation are replaced by a succession of interbedded shelly sandstones and mudstones (Tridwr Formation) that record the transition into a mid- to outer-shelf setting (Schofield et al., 2004). Upper parts of the Nantmel Mudstones Formation, above the Cautleyan–lower Rawtheyan shelly debrites of the Llwyncus Member (Schofield et al., 2004), pass similarly into the bioturbated shelfal muddy sandstones of the uppermost Katian (Rawtheyan) Cribarth Formation.

The Welsh Basin hosts the type section for the original UK Hirnantian Stage at Cwm Hirnant in North Wales (e.g. Fortey et al., 2000). Here and along the margins of the basin the distinctive shelly 'Hirnantia fauna' first appears above abrupt changes in sedimentary facies that record the impact on sea level and sediment supply of the first stages of an approaching glacial maximum event (e.g. Brenchley and Cullen, 1984). In the basin centre, where both shelly and graptolitic faunas are absent, it is the correlative facies contacts that are widely used as a proxy for the base of the UK stage (e.g. Davies et al., 2009) and, by extension, the revised international stage (e.g. Bergström et al., 2009). Correlation of the Hirnantian rocks of the shelf and basin has recently been revised by Davies et al. (2009). In the southern and central parts of the basin, the lower Hirnantian silty, sandy and commonly slumped turbiditic facies that form the lower part of the Yr Allt Formation are now equated with the Drosgol Formation of the Plynlimon area where the conglomeratic Pencerrigtewion Member records deposition at the time of maximum glacio-eustatic lowstand (Davies et al., 2009). The effects of slumping remain widespread in overlying Hirnantian Welsh basin rocks, but the onset of the post glacial-maximum rise in sea level is reflected in the finer grained facies that comprise the upper Yr Allt Formation and, in the Plynlimon area, the equivalent Brynglas Formation. It follows that the use here of the terms 'lower' and 'upper' Yr Allt Formation has specific meaning relating to Hirnantian glacioeustasy. The distinctive and widely recognised Mottled Mudstone Member (Cave and Hains, 1986; Temple, 1988), present at the base of the otherwise anoxic Cwmere Formation, records a significant post-glacial re-colonisation event felt throughout the Welsh Basin and along its margins that is linked to the first appearance of late Hirnantian *persculptus* biozone graptolites in Wales (Davies et al., 2009, 2013). The Cwmere Formation mudstones pass eastwards across the Tywi Anticline into the extensively slumped basin margin Twcytta Mudstones Formation with the base of the Silurian lying within these divisions.

The lithostratigraphy of Hirnantian shelfal facies preserved along the eastern margin of the Welsh Basin is predictably more complicated (e.g. Schofield et al., 2004; Barclay, 2005; Davies et al., 2009; Schofield et al., 2009). To the west of the Crychan Fault Belt, the lower Hirnantian burrowed sandstones and silty mudstones of the Ciliau Formation pass into wave-rippled Cwmcringlyn Formation sandstones. Transgressive later Hirnantian facies are represented by the interbedded thin sandstones and smooth mudstones of the trace fossil-rich Garth House

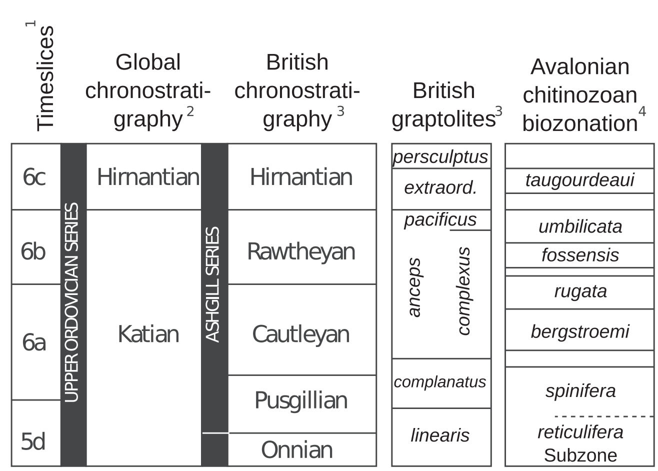

Fig. 3. The current Avalonian chitinozoan biozonal scheme and its correlation with British graptolite biozones and British and international chronostratigraphy. [1]Webby et al. (2004), [2]Cope (2007), [3]Fortey et al. (2000) and Bergström et al. (2009), [4]Vandenbroucke (2008a).

Formation (Fig. 2). However, when traced eastwards upper Katian (Rawtheyan) and lower Hirnantian strata are truncated by an unconformity that records emergence and erosion during the glacioeustatic lowstand; and here conglomerate and sandstone bodies (Cwm Clyd Sandstone and Glassallt-Fawr Sandstone formations) present below the base of the Garth House Formation record the subsequent late Hirnantian marine transgression. Within the overlying uppermost Hirnantian succession, weakly burrowed silty mudstones (Chwefri Formation) pass into thoroughly bioturbated sandy mudstones (Bronydd Formation) as part of a distal to proximal facies transition. Davies et al. (2009) correlate the burrow-mottled Ystradwalter Member at the base of the Chwefri Formation with the basinal Mottled Mudstone Member (see below).

3. Graptolites and shelly fossils

Though absent in lower Hirnantian (upper Ashgill) rocks of south-mid Wales, biostratigraphically significant graptolite assemblages are locally abundant in both the underlying Katian and overlying uppermost Hirnantian successions. Together these assemblages provide a key framework that allows the regional Welsh Basin chitinozoan biostratigraphy developed here to be compared with the British Avalonian scheme of Vandenbroucke (2008a).

Graptolites from the Dinas Island Formation and from the Sugar Loaf Member confirm the lower Katian *clingani* biozone. However, from the Cwm Degwel Mudstone Member at Frongoch (SN 076 410), Williams et al. (2003) record probable *Climacograptus tubuliferus*, a proxy for the middle Katian *Pleurograptus linearis* biozone, though *P. linearis* itself is not present. In the succeeding Nantmel Mudstones Formation graptolites have only been recovered from the 'Red Vein' anoxic units, but these confirm the *anceps* Biozone of late Katian age. Pugh (1923) records the index taxon *Dicellograptus anceps* along with *Orthograptus truncatus* var. *abbreviatus* and *Climacograptus scalaris* var. *miserabilis* in the Corris area assemblages. Those from the Cardigan–Llangrannog section lack the index fossil, but are dominated by *Orthograptus abbreviatus* with rarer '*Climacograptus*' cf. *supernus*, *Normalograptus miserablis* and fragmentary dicellograptids (Williams, 2001a, 2001b) and compare with similar assemblages recovered from the east of the basin (Davies et al., 1997). *O. abbreviatus* is present in the broadly coeval Sholeshook Limestone of the Whitland area of south Wales (Zalasiewicz et al., 1995).

In the Llandovery area, Cocks et al. (1984) report long ranging Upper Ordovician graptolites associated with a Rawtheyan shelly fauna from the upper part of the Tridwr Formation. Graptolites collected from the Cribarth Formation during this study include *O. abbreviatus* (sample TJC 09-06-01) from Garth Bank [SN 942 499] and *Normalograptus normalis* from Glasallt Farm, south of Llandovery, both consistent with the *anceps* biozone (Zalasiewicz et al., 2009).

The lower Hirnantian *extraordinarius* biozone has not been recognised in Wales, but the base of the upper Hirnantian *Normalograptus persculptus* biozone within the Mottled Mudstone Member provides an important marker horizon throughout the Welsh Basin (e.g. Jones, 1909; Pugh, 1923; Hendriks, 1926; Temple, 1988; Davies et al., 2013). Critically, *N. persculptus* biozone assemblages persist for some distance into the succeeding Cwmere Formation and have allowed Blackett et al. (2009) to chart progressive changes in the

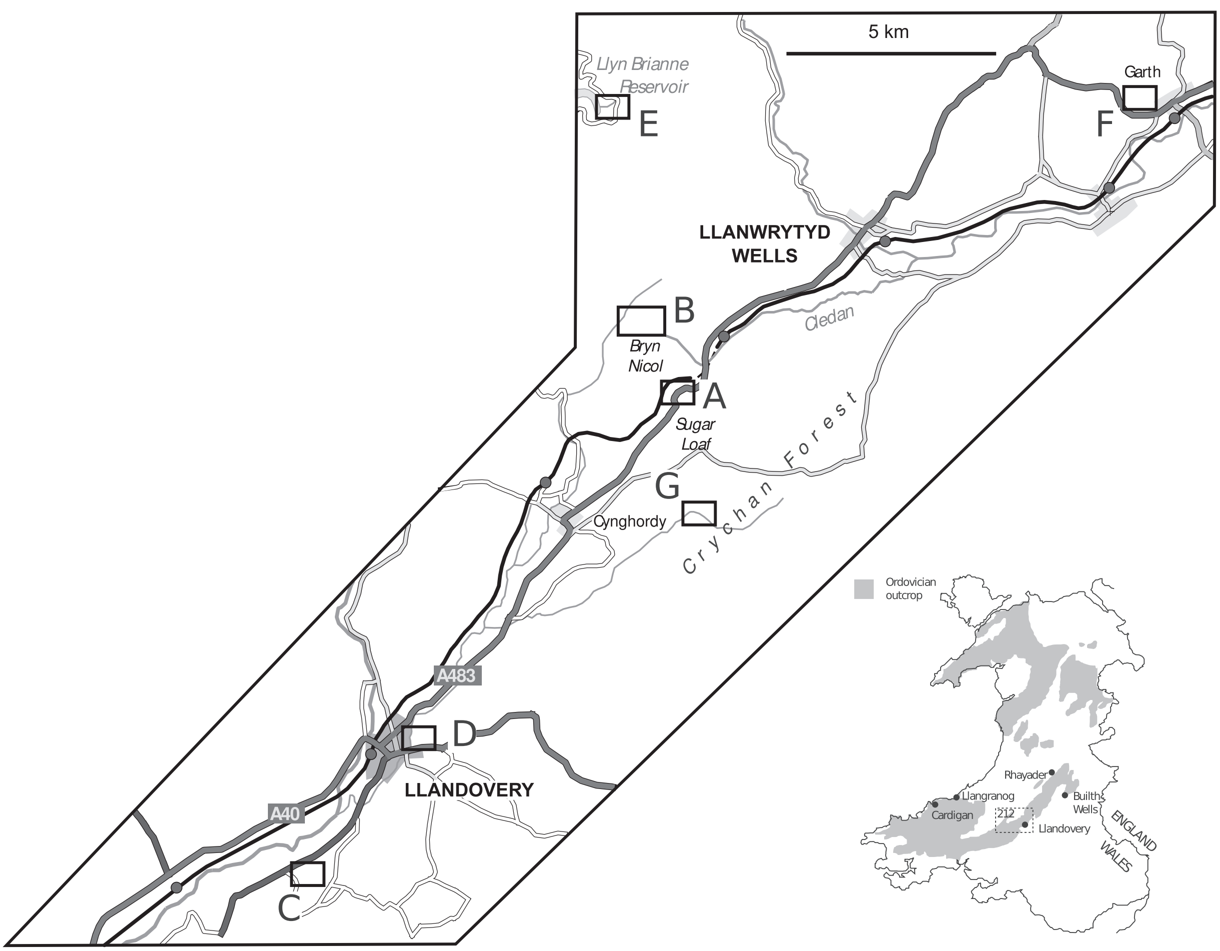

Fig. 4. Sample sections for chitinozoan biostratigraphy in the Tywi Anticline, Garth and Llandovery areas. A = Sugar Loaf section, B = Bryn Nicol section, C = Glasallt Fawr, D = A40 road section, E = Llyn Brianne reservoir samples, F = Garth House Formation Type locality, G = Crychan Forest section.

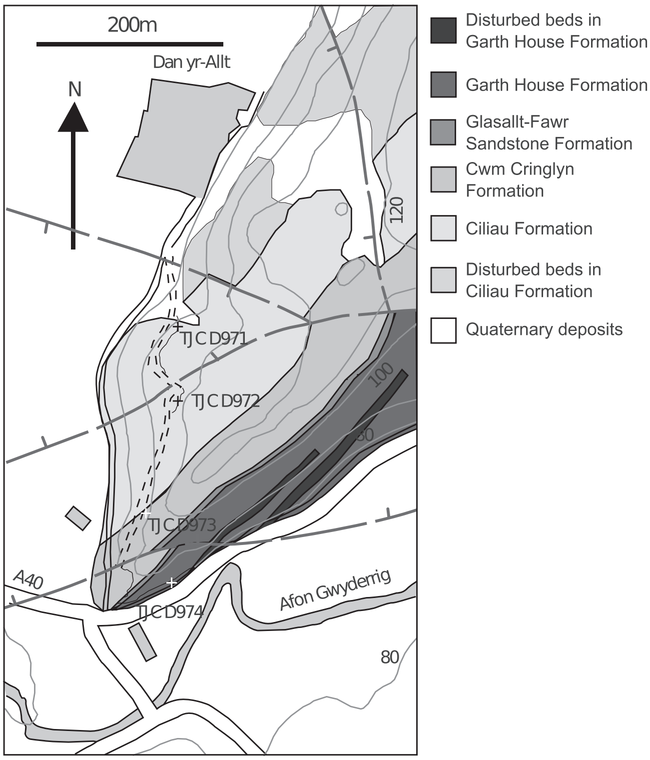

Fig. 5. Geological map and sample localities for the Dan–yr–allt and A40 road section, Llandovery (Section D) (after BGS, 2008).

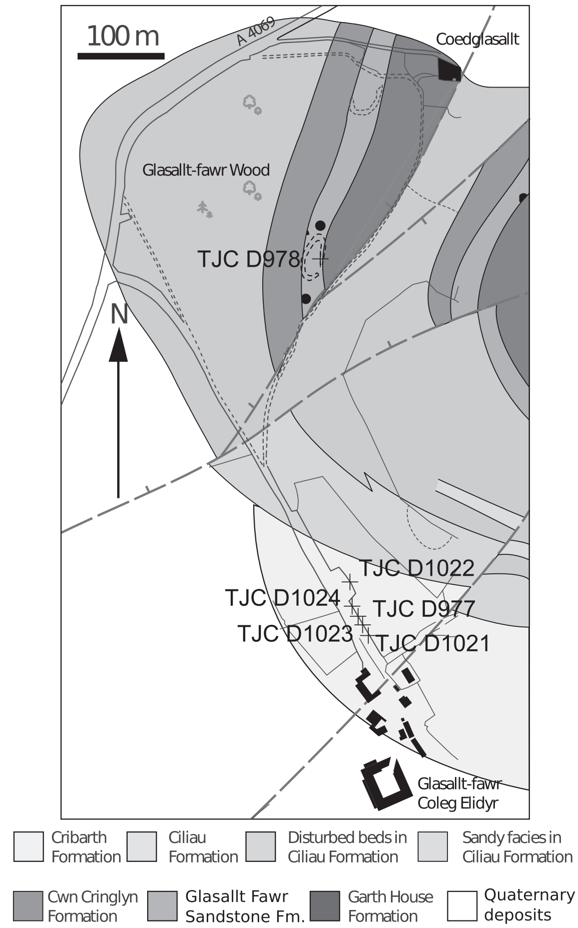

Fig. 7. Geological map and sample localities for the Glasallt Fawr area (Section C) (after BGS, 2008).

morphology of *Normalograptus? parvulus* for example at Cerrig Gwinion Quarry [SN 973 656] and Lynn Brianne [SN 816 493]. It is the morphotypes of this taxon present in lower levels of the Llandovery area Chwefri Formation that support the correlation of the underlying Ystradwalter Member with the Mottled Mudstone Member (Davies et al., 2009). In addition, Cocks et al. (1984) report a form of *Climacograptus normalis* from a low level in the Bronydd Formation consistent with the *persculptus* biozone, but certainly no higher than the basal Silurian *acuminatus* biozone (now *ascensus-acuminatus* Biozone; see Zalasiewicz et al., 2009).

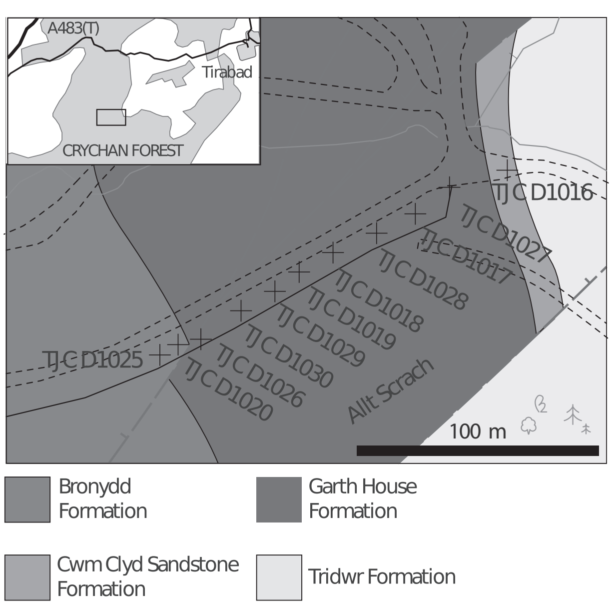

Fig. 6. Geological map and sample localities for the Crychan Forest area (Section G) (after BGS, 2008).

A shelly fauna collected from the Pen Derlwyn facies of the Bryn Nicol Formation has yielded a diverse fauna suggestive of a Rawtheyan age (Rushton, 1994). The diverse, reworked shelly fauna recovered from the Llwyncus debrite of the Garth section is of Cautleyan to early Rawtheyan aspect (Schofield et al., 2004) and a shelly fauna recovered from the uppermost Cribarth Formation at Glassallt Fawr includes the trilobite *Brongniartella* cf. *robusta* which, according to Williams and Wright (1981, p. 8), indicates a "very high Rawtheyan age". From the Garth area, Williams and Wright (1981) record the distinctive cool water '*Hirnantia* fauna' from rocks now included in the Ciliau Formation and Cocks et al. (1984; also Woodcock and Smallwood, 1987) report similar Hirnantian shelly assemblages from levels within the former Scrach Formation that are now viewed as part of the Cwmcringlyn Formation (see discussion by Davies et al., 2009).

4. Chitinozoan biostratigraphical and chronostratigraphical framework

Vandenbroucke (2008a) has developed a chitinozoan biostratigraphy for the upper Katian and Hirnantian (Ashgill) from historical type sections in the Anglo-Welsh area, including the Cautley District, Pus Gill (Vandenbroucke et al., 2005), Greenscoe (Van Nieuwenhove et al., 2006), Whitland (Vandenbroucke et al., 2008b), Cwm Hirnant and the Wye Valley (Vandenbroucke et al., 2008a). Six chitinozoan biozones, with two subzones, were recognised by Vandenbroucke (2008a) (Fig. 3) who provided the following criteria for their definition:

The *Fungochitina spinifera* biozone corresponds to the total range of the index fossil. In the Cardigan–Llangrannog section it has tentatively been recognised in the *Dicranograptus clingani* biozone (Vandenbroucke

Table 1
Chitinozoan abundance for the Cardigan–Llangranog composite coast section. [1]Vanmeirhaeghe (2006), [2]Vandenbroucke (2008b).

	TJC D953	TJC D940	TJC D1006	TJC D1007	TJC D941	TJC D942	TJC D943	TJC D1003	TJC D1004	TJC D1013 1014	TJC D1015	TJC D1009	TJC D1001	TJC D1000	TJC D979	TJC D955-1002	TJC D967	TJC D968	TJC D957	TJC D956	TJC D1010	TJC D1005	TJC D949	TJC D946	TJC D947	TJC D948
Cyathochitina campanulaeformis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	1	–	–	–	3	–	–
Cyathochitina cf. *campanulaeformis*	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	2	–	1	3	–	–
Cyathochitina kuckersiana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
Cyathochitina cf. *kuckersiana*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
Cyathochitina calix	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
Cyathochitina cf. *reticulifera*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyathochitina sp.	5	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	3	–	–
Saharochitina cf. *fungiformis*	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Saharochitina sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–
Tanuchitina bergstroemi	–	–	1	–	–	1	1?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tanuchitina sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–
Hercochitina sp.	1	–	1	–	–	2	1	1	–	8	6	–	–	5	–	2	–	–	2	–	5	1	–	–	–	–
Hercochitina cf. *normalis*	–	–	–	–	–	–	–	–	–	–	–	–	–	1	10	2	2	–	–	–	–	–	–	–	–	
Hercochitina aff. *normalis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	1	–	–	–	–	–
Hercochitina cf. *seriespinosa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	1	–	–	–	–	–	–
Hercochitina aff. *seriespinosa*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–	–
Hercochitina cf. *longi*	–	–	–	–	–	–	–	–	–	5	3	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–
Hercochitina minuta	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Hercochitina sp. A[1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	2	–	–
Hercochitina cf. *grandispinosa*	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ancyrochitina sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	1	–	–	–	–	1	–	–
Bursachitina umbilicata	–	–	–	–	–	–	–	–	–	16	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Spinachitina penbryniensis	–	–	–	–	–	–	4	–	6	35	21	–	–	–	14	–	–	–	1	2	11	–	–	–	–	–
Spinachitina coronata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–
Spinachitina cf. *fossensis*	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spinachitina fossensis	–	–	–	–	–	–	2	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Spinachitina cf. *bulmani*	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spinachitina sp. 2[2]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
Spinachitina sp. A[2]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Spinachitina sp. 4[2]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Spinachitina sp.	–	–	1	–	–	–	1	–	–	–	3	1	–	–	–	–	1	–	1	–	–	–	–	1	–	–
Rhabdochitina gracilis	–	–	–	–	–	–	–	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Conochitina rugata	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Conochitina cf. *homoclaviformis*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	2	–	–
Conochitina sp.	–	–	2	–	–	–	1	4	1	1	–	1	–	–	–	–	–	1	3	2	–	–	–	–	–	–
Belonechitina ceredigionensis	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	41	–	–	–	–
Belonechitina cf. *americana*	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Beloneochitina cf. *gamachiana*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	2	–	–	–	–	–	–
Belonechitina llangrannogensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15	–	4	–	–
Belonechitina wessenbergensis	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–
Belonechitina sp. 7[2]	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Belonechitina sp. 12[2]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–
Belonechitina sp.	–	1	–	–	–	–	4	1	–	1	2	–	–	6	–	–	–	–	–	–	3	14	–	6	–	2
Laufeldochitina sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	2	–	–
Eisenackitina sp.	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Desmochitina cocca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–
Desmochitina minor	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	5	5
Chitinozoa indet.	15	–	11	–	2	4	93	6	11	7	17	–	1	10	–	–	2	1	–	8	9	9	2	1	3	–
Total number of chitinozoans	22	3	17	–	5	11	117	13	18	78	65	2	1	35	50	12	10	8	8	16	33	84	9	47	8	7
Amount of dissolved rock (g)	30	20.7	17.4	20.9	21.3	20.7	26.2	20.3	13.2	39.9	20.2	16.6	20.5	23.8	30.5	52	79.9	79.8	30	30	20.3	21	97.4	49.2	50.9	44.1

et al., 2008b). In N. England, the *F. spinifera* biozone straddles the Caradoc–Ashgill boundary and is dated as mid Katian (Onnian to Pusgillian) of the British scheme (Fortey et al., 2000, time slice 5d–6a of Webby et al., 2004). In Avalonia, *Saharochitina fungiformis* is taken as a proxy for the *F. spinifera* biozone. Other important associated taxa corresponding to this biozone are *Lagenochitina baltica*, *Lagenochitina prussica*, *Belonechitina robusta*, *Spinachitina* ?*coronata* and *Conochitina* ?*incerta*.

The *Armoricochitina reticulifera* subzone, defined by Nõlvak and Grahn (1993) in Baltoscandia, of the *F. spinifera* biozone has been recognised in the Cardigan area associated with graptolites of the *Dicellograptus morrisi* subzone of the *D. clingani* biozone.

The *Tanuchitina bergstroemi* biozone in Avalonia is defined as corresponding to the first appearance datum (FAD) of *T. bergstroemi* to the first occurrence of *Conochitina rugata*, the index fossil of the overlying biozone. *Belonechitina americana* is an associated taxon in this biozone. In the aforementioned Frongoch locality of the Cardigan area, numerous fragments cautiously attributed to the biozone index fossil (which is a very fragile species) correspond to the middle Katian *P. linearis* biozone (Vandenbroucke et al., 2008b). Vandenbroucke et al. (2005) viewed the *T. bergstroemi* biozone as mid-late Katian (~Cautleyan) in age, but on recognising the implications of this for the correlation of the Welsh Basin succession, Vandenbroucke et al. (2008b, p. 211) have subsequently advised that “confirmation of the presence of *T. bergstroemi* at Frongoch, and in equivalent strata elsewhere, should be viewed as an urgent requirement”.

The *C. rugata* biozone in Avalonia is defined as the total range of the index fossil. It corresponds to the *C. rugata* biozone in Baltoscandia (Nõlvak and Grahn, 1993) and is dated late mid to late Katian (late Cautleyan to early Rawtheyan).

The *Spinachitina fossensis* biozone is a partial range biozone defined by the first appearance of *S. fossensis* to the first appearance of *Bursachitina umbilicata*, the overlying biozone's index taxon. In the Cautley district of northern England, this biozone occurs in the middle of the shelly fauna Zone 6 of Ingham (1966). Rickards (2002) assigned associated graptolites to the *P. linearis* biozone, although the upward revision of biozonal boundaries implied by this has not been generally accepted (e.g. Zalasiewicz et al., 2009; Vandenbroucke et al., 2013). Associated taxa include *Belonechitina* sp. 8 Vandenbroucke, 2008b and

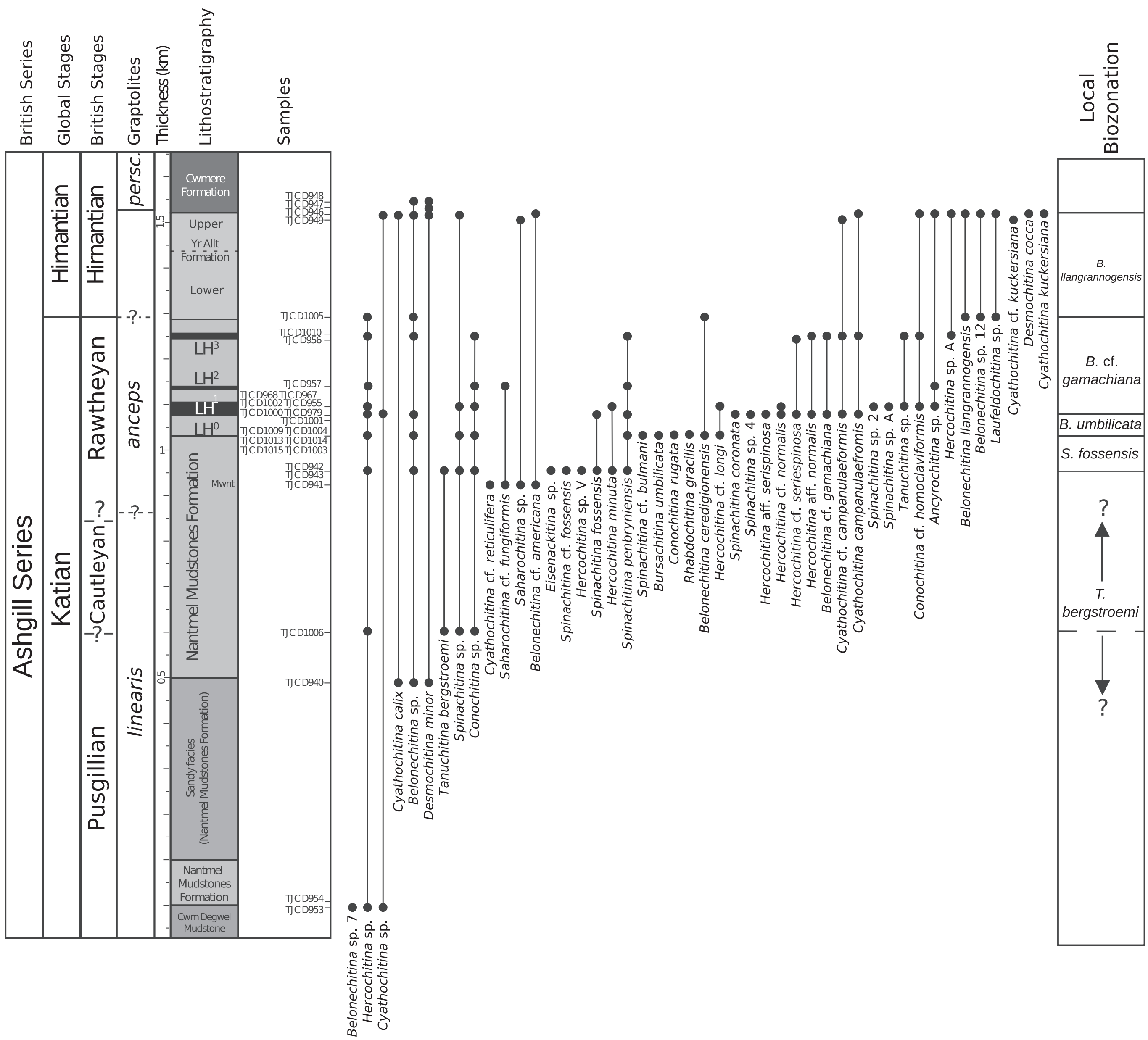

Fig. 8. Chitinozoan ranges in the middle Katian to Hirnantian (Ashgill) succession of the Cardigan Bay area (Cardigan to Llangrannog section) and interpreted biozonation.

Table 2
Chitinozoan abundance from the Llandovery region composite section. [1]Vanmeirhaeghe (2006), [2]Vandenbroucke (2008b).

	Sugar loaf section		Bryn Nicol section						Cribarth Formation, Glasallt Fawr				
	TJC D952	TJC D950	TJC D1033	TJC D960	TJC D959	TJC D1032	TJC D1031	TJC D958	TJC D1021	TJC D1023	TJC D977	TJC D1024	TJC D1022
Hercochitina sp. 1[1]	–	–	–	–	–	–	–	–	–	–	4	–	1
Hercochitina aff. *seriespinosa*	–	1	–	3	–	1	–	–	–	–	–	–	–
Hercochitina cf. *seriespinosa*	–	–	–	–	–	–	–	–	–	–	1	–	–
Hercochitina aff. *normalis*	–	–	1	–	1	2	–	–	–	–	–	–	–
Hercochitina cf. *normalis*	–	–	–	–	–	–	–	1	–	–	–	–	–
Hercochitina cf. *longi*	–	–	2	–	4	–	–	–	–	–	4	–	–
Hercochitina sp.	2	4	7	3	24	–	5	1	1	–	4	1	–
Belonechitina ceredigionensis	–	–	–	–	–	–	–	–	–	1	–	–	–
Belonechitina capitata	–	–	–	–	–	–	–	–	1	–	4	–	–
Belonechitina cf. *gamachiana*	–	–	–	–	–	–	–	–	–	–	–	1	–
Belonechitina sp. 7[2]	1	–	–	–	–	–	–	–	–	–	–	–	–
Belonechitina sp.	1	1	–	1	–	–	–	–	–	–	3	–	–
Cyathochitina campanulaeformis	1	–	–	2	–	–	–	–	–	–	–	1	–
Cyathochitina cf. *campanulaeformis*	–	–	8	14	–	–	–	–	–	–	–	–	–
Cyathochitina cf. *kuckersiana*	–	–	2	–	–	–	–	–	–	–	–	–	–
Cyathochitina calix	–	–	1	–	–	–	–	–	–	–	–	–	–
Cyathochitina sp.	–	1	2	–	1	–	3	3	–	1	1	1	–
Desmochitina erinacea	–	–	–	–	–	–	2	–	–	–	–	–	–
Desmochitina minor	–	–	–	1	–	–	–	–	–	2	–	–	–
Desmochitina cocca	–	2	–	–	–	–	–	–	–	–	–	–	–
Desmochitina sp.	1	–	–	–	–	–	–	–	–	–	–	–	–
Spinachitina fossensis	–	–	9	–	–	–	4	–	–	–	–	–	–
Spinachitina cf. *fossensis*	–	–	3	2	1	1	–	–	–	–	–	–	–
Spinachitina cf. *bulmani*	–	1	–	–	–	–	–	–	–	–	–	–	–
Spinachitina coronata	–	–	–	–	–	–	–	–	–	1	–	4	–
Spinachitina sp.	–	–	–	–	–	–	–	1	–	–	–	–	–
Laufeldochitina sp.	1	–	–	–	–	–	1	–	–	–	–	–	–
Tanuchitina sp.	–	–	–	–	1	–	–	2	–	–	–	–	–
Conochitina homoclaviformis	3	4	–	–	–	–	–	–	–	–	–	–	–
Conochitina sp. 1	1	3	–	–	–	–	–	–	–	1	2	–	–
Conochitina sp.	–	5	3	–	–	–	–	1	–	–	–	–	–
Ancyrochitina sp.	–	–	–	1	–	–	–	–	–	–	–	–	–
Saharochitina sp.	–	–	–	–	–	–	2	1	–	–	–	–	–
Chitinozoa indet.	2	20	3	8	10	4	7	–	2	1	1	–	–
Total number of chitinozoans	13	42	41	35	43	8	26	10	4	7	24	8	1
Amount of dissolved rock (g)	30	30	12.4	10	12	9	12.9	15	15.4	14.6	41.3	14.6	11.8

Spinachitina sp. 4 Vandenbroucke, 2008b. This biozone has been recorded from the Condroz inlier of Belgium (Vanmeirhaeghe and Verniers, 2004) but is not known outside Avalonia.

The *B. umbilicata* biozone is defined as the total range of the index taxon. It has also been recorded from Condroz inlier of Belgium (Vanmeirhaeghe and Verniers, 2004) and from the Kaugatuma core in Estonia (Baltica) by Kaljo et al. (2008). It is of late Katian (mid- to late-Rawtheyan) age.

Vandenbroucke (2008a) did not recognise the Laurentian and Baltoscandian *Hercochitina gamachiana* biozone in Avalonia, but discoveries made as part of this study suggest it may be represented in the Welsh Basin. However, its age is disputed as being either exclusively Hirnantian (Achab et al., 2011, 2013) or as partially Katian and Hirnantian (Hints et al., 2004; Kaljo et al., 2008). It is defined in Laurentia by Achab (1989) as the partial range of *B. gamachiana* between its first appearance and that of the index of the succeeding biozone, *Spinachitina taugourdeaui*. In Baltoscandia, Nõlvak (1999) defines it as corresponding to an interval between the *C. rugata* and *S. taugourdeaui* biozones.

The *Ancyrochitina merga* biozone, is defined in Avalonia as corresponding to the total range of the index fossil and is of late Katian age (Vandenbroucke, 2008a). This is the same definition as for the *A. merga* subzone in northern Gondwana where it was first defined (Paris, 1990). *Euconochitina lepta* is an associated chitinozoan species. It is of late Katian (late Rawtheyan) age.

The *S. taugourdeaui* biozone is a partial range biozone. Its base in Baltoscandia (Nõlvak and Grahn, 1993), is defined by the first appearance of *S. taugourdeaui* and its top by the first appearance of *Conochitina scabra*. The index taxon was first recognised in Avalonia in North Wales where it was restricted to the Hirnant Limestone (Vandenbroucke et al., 2008a). Because of its co-occurrence there, *Belonechitina* sp. 11 (Vandenbroucke, 2008a, 2008b) was considered to serve as a correlative proxy taxon for the *S. taugourdeaui* biozone in Wales (Vandenbroucke, 2008a), Here we define *Belonechitina* sp.11 as a new species and erect a new biozone from its partial range, the *Belonechitina llangrannogensis* biozone.

5. Sampling and treatment

A total of 64 samples were collected from localities representing a shelf to basin transect from the middle–upper Katian (uppermost Caradoc–Ashgill). Localities were chosen on completeness of section (lack of faulting), exposure and accessibility. Twenty-seven samples representative of basinal facies came from the Cardigan Bay region, from the Cwm Degwel Mudstone Member (oldest), the Nantmel Mudstones (including the 'Red Vein'), both the lower and upper Yr Allt Formation and the Cwmere Formation (youngest) (Fig. 3). This sampling programme complements that of Vandenbroucke et al. (2008b) who collected from the underlying early Katian (Caradoc) succession up to and including the Cwm Degwel Mudstone Member.

The remaining 37 samples were obtained from seven sections (Figs. 4, 5, 6 and 7) located in the east of the basin and along its marginal shelf. These included surface exposures in basin facies (Sugar Loaf Member and Nantmel Mudstones Formation), basin margin facies (Pen Derlwyn and Coed Ifan facies of the Bryn Nicol Formation) and the shelfal successions of the Garth and Type Llandovery areas (Tridwr,

Table 3
Chitinozoan abundance of from the Llandovery region composite section. [1]Vanmeirhaeghe (2006), [2]Vandenbroucke (2008b). LB = 'Smooth Mudstones', Llyn Brianne reservoir, GH = Garth House Formation, Garth House, CCy = Cwm Clyd Sandstone Formation, Glasallt Fawr.

	A40 road section				LB	GH	CCy	Brynffo Forest section											Dolaucothi M8 core					
	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC	TJC
	D971	D972	D973	D974	D975	D976	D978	D1016	D1027	D1017	D1028	D1018	D1019	D1029	D1030	D1026	D1020	D1025	D980	D981	D982	D983	D984	D985
Hercochitina aff. seriespinosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–
Hercochitina sp.	–	1	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Belonechitina micracantha	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Belonechitina llangrannogensis	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–
Belonechitina ceredigionensis	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Belonechitina capitata	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Belonechitina sp. A[2]	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Belonechitina sp. 12[2]	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Belonechitina sp.	–	2	–	2	–	5	–	3	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Lagenochitina cf. *ponceti*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Lagenochitina sp.	–	–	–	–	1	3	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
Cyathochitina campanulaeformis	–	1	–	–	–	4	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyathochitina cf. campanulaeformis	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	4	–	–	–	10	8
Cyathochitina kuckersiana	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–
Cyathochitina cf. reticulifera	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyathochitina calix	–	–	–	–	–	2	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyathochitina sp.	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Desmochitina juglandiformis	–	–	–	–	–	4	–	–	–	–	–	–	–	3	–	–	–	1	–	–	–	–	–	–
Desmochitina erinacea	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Desmochitina minor	–	–	–	–	–	–	–	21	–	–	1	–	1	9	3	7	–	3	–	–	–	–	–	–
Desmochitina cf. minor	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–
Desmochitina cocca	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Desmochitina sp.	–	–	–	–	1	1	1	5	2	–	–	–	–	–	5	12	3	4	–	–	–	–	–	–
Spinachitina cf. *taugourdeaui*	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Spinachitina sp. 4[2]	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spinachitina sp.	–	–	–	–	1	2	–	6	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Laufeldochitina lardeuxi	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Laufeldochitina sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Tanuchitina sp. A[1]	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tanuchitina sp.	–	–	2	–	–	2	–	2	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Conochitina sp. 1	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bursachitina sp.	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Eisenackitina inconspicua	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eisenackitina cf. *rhenana*	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eisenackitina sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Siphonochitina sp.	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ancyrochitina sp.	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	7	14
Ancyrochitina cf. *primitiva*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8
Chitinozoa indet.	14	3	1	5	11	151	7	6	–	–	2	–	–	–	–	1	–	2	–	–	–	5	3	1
Total number of chitinozoans	17	7	5	10	18	200	12	54	4	–	3	–	1	17	8	25	5	14	18	–	–	5	20	31
Amount of dissolved rock (g)	25.3	27.7	25.9	33	46.8	32.6	35.9	14.2	13.8	12.1	16.4	12.7	13.9	15.3	16.5	14.5	13.4	13.3	18.3	15.6	25.2	11.3	21.2	11.7

Cribarth, Ciliau, Cwmcringlyn, Cwm Clyd Sandstone, Glasallt-Fawr Sandstone, Garth House and Bronydd formations; Fig. 4). In addition, samples from the basinal Yr Allt and Cwmere formations were obtained from the Dolaucothi M8 Borehole, Pumsaint. The sampling in the Llandovery area compliments the study by Davies et al. (2013) that focused principally on Silurian strata. All sample localities are listed in Appendix II. Extraction of organic residues followed the procedure outlined by Paris (1981).

6. Results

6.1. Cardigan Bay (Cardigan to Llangrannog)

A total of 678 chitinozoans were recovered from 27 samples from the coast section between Cwm Degwel, Cardigan and Traeth-yr-Ynys Lochtyn, Llangrannog (Fig. 1). Abundance data for the Cardigan Bay region is given in Table 1 and the range of recovered taxa is presented in Fig. 8. The preservation of chitinozoans from the Cardigan–Llangrannog coast section varies from poor, crushed and broken specimens, as typically recovered from oxic facies, to slightly worn 3-dimensional vesicles maintaining diagnostic features. The best material was recovered from the anoxic units of the Red Vein (samples TJC D979, TJC D1015) and dark mudstones of the lower Yr Allt Formation at Llangrannog (samples TJC D946 and TJC D1005). Poor chitinozoan recovery may possibly be attributed to high sedimentation rate and oxic palaeoenvironment in the Nantmel Mudstones Formation and the Hirnantian sediments accounting for the best yields coming from the anoxic units of the Katian Red Vein (LH^0–LH^3 of Challands et al., 2009).

6.2. Eastern sections (Tywi Anticline, Garth and Llandovery areas)

A total of 736 chitinozoans were obtained from the 37 samples (including the Bryn Nicol section and Dolaucothi M8 core) collected in this region. The numerical results are presented in Tables 2 and 3 and the chitinozoan ranges are plotted on a composite range chart (Fig. 9). Chitinozoan preservation is variable from section to section in this region. Multiple samples taken from the same formation along strike were noted to vary considerably in chitinozoan abundance and state of preservation. For example, in the Garth House Formation the majority of specimens from the Y-Grug - A40 road section are flattened (TJC D971, TJC D974) whereas from the formation's type locality on Garth Bank (TJC D976) numerous 3-dimensionally preserved chitinozoans

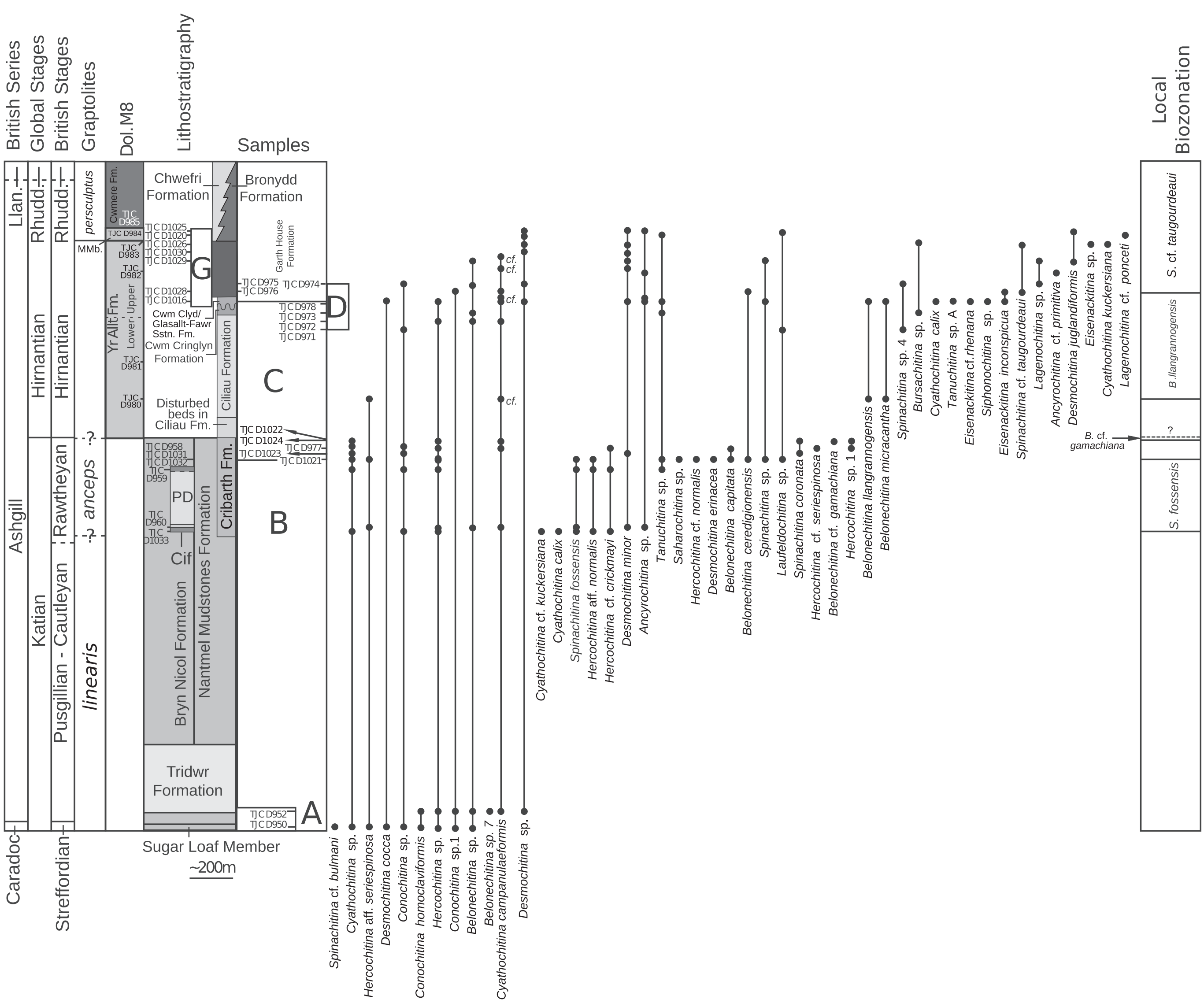

Fig. 9. Chitinozoan ranges in the middle Katian (upper Caradoc) to Hirnantian (Ashgill) succession of the Tywi Anticline, Garth and Llandovery areas and interpreted chitinozoan Biozonation. PD = Pen Derlwyn facies; CIF = Coed Ifan facies of the Bryn Nicol Formation.

were recovered. Only one sample (sample TJC D951) from the Nantmel Mudstones Formation of the Sugar Loaf section (Section A, Fig. 4) was barren.

7. Biozonation

Five Ordovician biozones can be recognised in the Cardigan Bay–Garth/Llandovery transect: four formerly known Avalonian biozones and one Laurentian biozone not previously recorded from Avalonia.

7.1. T. bergstroemi biozone

The lowest recognised biozone is the *T. bergstroemi* biozone, originally defined by Nõlvak and Grahn (1993) in Baltoscandia as corresponding to the total range of the index fossil. *T. bergstroemi* is recorded in the Cardigan area from samples TJC D946 (Gwbert) to TJC D943 (Pen y Craig). Samples stratigraphically below these levels did not yield any biostratigraphically useful chitinozoans. The associated taxon *B. americana* was recovered within the range of *T. bergstroemi* at Mwnt (sample TJC D941) and also much higher stratigraphically in the Yr Allt Formation (sample TJC D946). Neither *T. bergstroemi* nor the associated *B. americana* were recovered in the Llandovery area.

A single occurrence of the index for the *C. rugata* biozone was recorded in LH^0 (sample TJC D1015), but occurs above the base of the S. *fossensis* Biozone and is coincident with the FAD of *B. umbilicata*. *C. ? rugata* has also been recorded alongside *B. umbilicata* in the Cautley district of northern England by Vandenbroucke et al. (2005), and Kaljo et al. (2008) record *B. umbilicata* from the rugata Biozone from the Kaugatuma core. From these observations, we suggest the *C. rugata* biozone in Avalonia, and possibly Baltoscandia, should be redefined as a partial range biozone between the first appearance of the index fossil and the first appearance of *S. fossensis*; with *C. rugata* extending through the *S. fossensis* and into the *B. umbilicata* zone.

7.2. S. fossensis biozone

This biozone is recognised in both the Cardigan Bay and Tywi Anticline areas. In the former area the base is marked by the first appearance of *S. fossensis* in sample TJC D943 (Pen y Craig) and the top is marked by the first appearance of *B. umbilicata* from sample TJC D1013 (LH^0), the index taxon of the overlying biozone. In the Tywi Anticline area, the

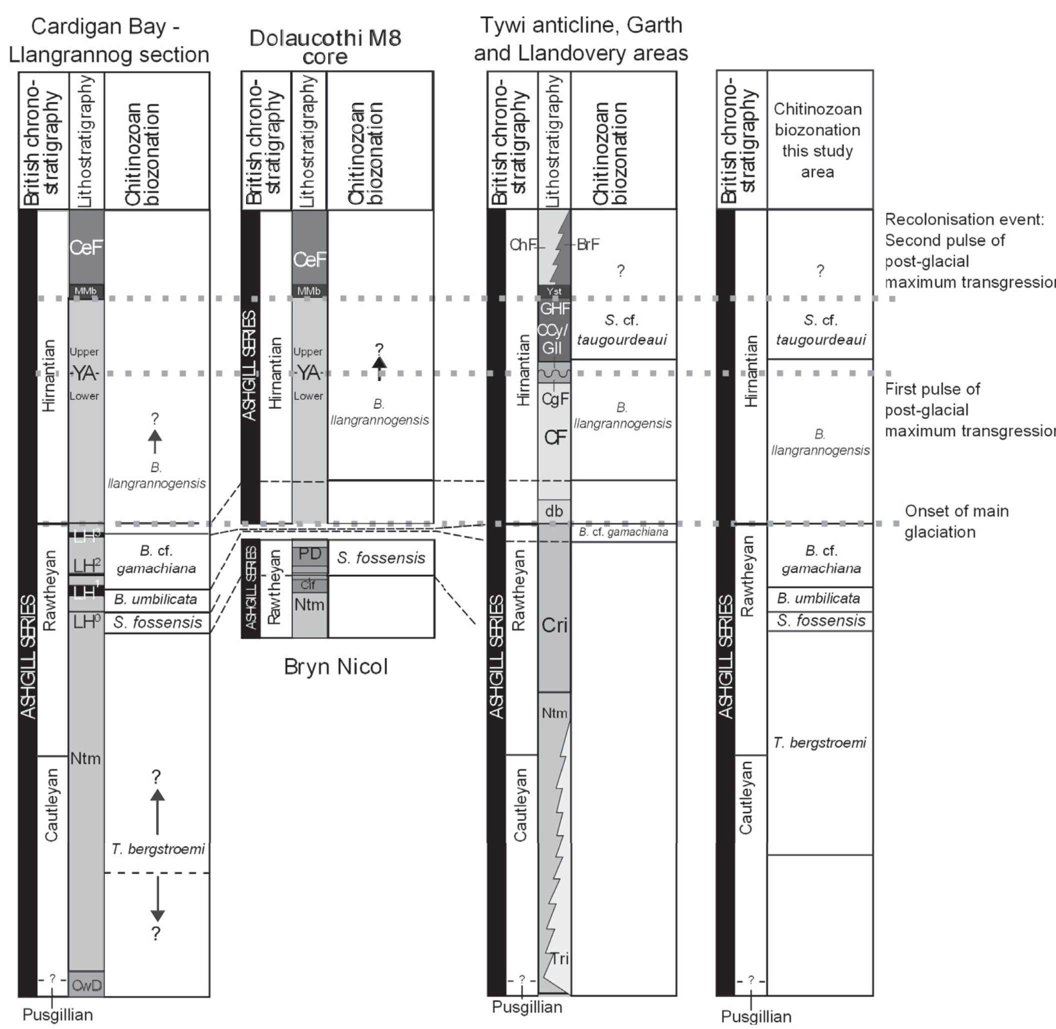

Fig. 10. Correlation of regional chitinozoan biozones between sections in the Cardigan–Llangrannog sections (Cardigan Bay) and Tywi Anticline, Garth and Llandovery areas and the revised composite chitinozoan biozonation scheme for the upper Katian and Hirnantian (Ashgill) Stages of the Welsh Basin. BrF = Bronydd Formation; CCy = Cwm Clyd Sandstone Formation; CeF = Cwmere Formation; CF = Ciliau Formation; CgF = Cwmcringlyn Formation; ChF = Chwefri Formation; Cif = Coed Ifan facies of the Bryn Nicol Formation; Cri = Cribarth Formation; CwD = Cwm Degwel Mudstone Member; db = disturbed beds of the Ciliau Formation; GHF = Garth House Formation; Gll = Glasallt-Fawr Sandstone Formation; LH^{0-3} = Laminated hemipealgite units 0–3 of the Nantmel Mudstones Formation; Ntm = Nantmel Mudstones Formation; MMb = Mottled Mudstone Member of the Cwmere Formation; PD = Pen Derlwyn facies of the Bryn Nicol Formation; SLM = Sugar Loaf Member; Tri = Tridwr Formation and YA = Yr Allt Formation, Yst = Ystrad Walter Formation.

first occurrence of *S. fossensis* is in the Nantmel Mudstones Formation at Bryn Nicol (sample TJC D958).

7.3. *B. umbilicata* biozone

This biozone is defined by the total range of the index taxon which in the Cardigan Bay region is from sample TJC D1013 to TJC D1015 and is restricted to LH^0. Taxa consistent with this biozone were not recorded in the Garth–Llandovery area.

7.4. *Belonechitina* cf. *gamachiana* biozone

The original *B. gamachiana* biozone erected in Laurentia by Achab (1989) and subsequently recognised in Baltoscandia (Nõlvak, 1999), corresponds to the partial range of *B. gamachiana* between its first appearance and the appearance of *S. taugourdeaui*, the index species of the succeeding biozone. In Baltoscandia, this corresponds to upper Pirgu (uppermost Rawtheyan, uppermost Katian) (Nõlvak, 1999) to lowest Hirnantian. The original *B. gamachiana* biozone was not recorded in Avalonia by Vandenbroucke (2008a). However, he records specimens of *H.* cf. *gamachiana* from the overlying *S. taugourdeaui* biozone in Cwm Hirnant and specimens doubtfully identified as *H.* aff. *gamachiana* from Hirnantian rocks in the Claerwen Valley (Vandenbroucke et al., 2008a). In the present study, *Belonechitina* cf. *gamachiana* was recovered in both the Cardigan and Llandovery areas. In the Cardigan area its FAD was in sample TJC D979 (Nantmel Mudstones Formation, LH^1) and in eastern sections in sample TJC D1023 (Cribarth Formation). This warrants tentative recognition of the biozone in Wales. However, pending the recovery of the global index taxon, here we erect a local *Belonechitina* cf. *gamachiana* Biozone defined by the partial range of *B.* cf. *gamachiana*, from its first appearance to the FAD of *B. llangrannogensis* n. sp., the index species of the succeeding newly erected biozone (but see discussion below). How this biozone relates to the original *B. gamachiana* biozone is to be determined.

7.5. *B. llangrannogensis* n. sp. biozone

In the Welsh Basin *B. llangrannogensis* n. sp. (as defined herein) appears to have a restricted stratigraphical range. An eponymous biozone was not recognised in Avalonia by Vandenbroucke (2008a), but the taxon (*Belonechitina* sp. 11 of Vandenbroucke, 2008a, 2008b) was noted to have the potential for biostratigraphical use. At Hirnant Quarry in the north Wales it occurs with *S. taugourdeaui* and in Cerrig Gwinion Quarry (Tywi Anticline), it occurs in the upper Yr Allt Formation below the Mottled Mudstone Member FAD of *persculptus* biozone graptolites (Vandenbroucke et al., 2008b). In the Cardigan Bay area it ranges from the lowermost Yr Allt Formation at Traeth Penbryn (sample TJC D1005), where it enters above the local last appearance of *B.* cf. *gamachiana*, into the upper Yr Allt Formation at Llangrannog (sample TJC D946). It appears to have a more restricted range in eastern sections first appearing in the lower Yr Allt Formation (sample TJC D980, Dolaucothi M8 Borehole) and ranging no higher than the Glasallt-Fawr

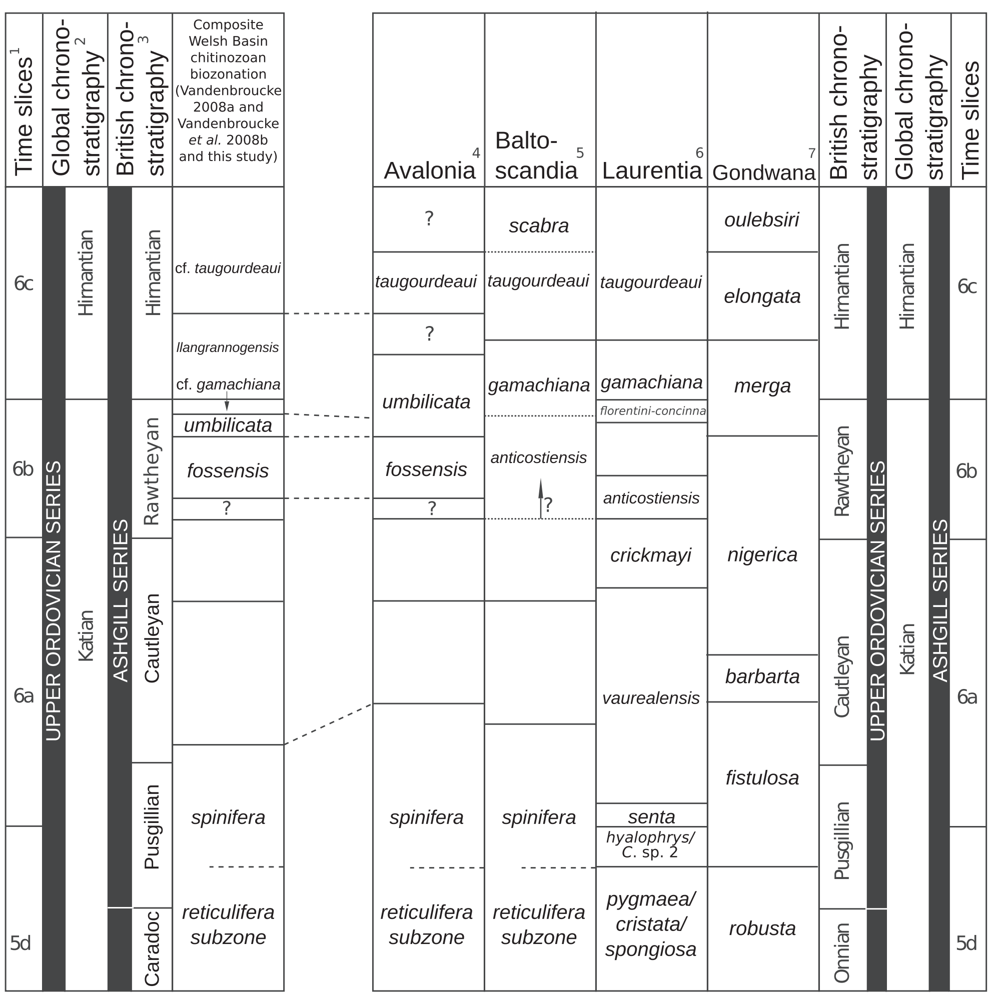

Fig. 11. Correlation of the revised Welsh Basin chitinozoan biozonal scheme (this study and Vandenbroucke (2008a, 2008b) and Vandenbroucke et al. (2008b)) with those of other Avalonian sections (Cautley Inlier, Condroz Inlier), Baltoscandia, Gondwana and Laurentia. In this study the *rugata* biozone is not recognised in the Welsh Basin. [1]Webby et al. (2004), [2]Bergström et al. (2006), [3]Fortey et al. (2000), [4]Vandenbroucke (2008a), [5]Nõlvak (1999), [6]Soufiane and Achab (2000), Achab (1978), Achab et al. (2013), [7]Paris (1990).

Sandstone Formation in Glasallt Fawr Wood (sample TJC D978). Within the Welsh Basin, the partial range of *B. llangrannogensis* n. sp. defines a local range biozone corresponding to the FAD of *B. llangrannogensis* n. sp. to the FAD of *Spinachitina* cf. *taugourdeaui*, the index taxon of the overlying biozone. Its occurrence between the *B.* cf. *gamachiana* and *S.* cf. *taugourdeaui* biozones implies an early Hirnantian age for this newly recognised biozone.

7.6. Spinachitina cf. taugourdeaui biozone

This biozone is recognised in the Garth area by the first appearance of *S.* cf. *taugourdeaui* in sample TJC D976 (Garth House Formation, Garth House). The same taxon occurs stratigraphically higher in the Garth House Formation in the Llandovery area (Crychan Forest sample TJC D1026), 2 m below the base of the overlying Bronydd Formation and, from the same section, Davies et al. (2013) report poorly preserved chitinozoans from the base of the Garth House Formation which they too assign to this biozone. These occurrences in post-dating the initial post-glacial maximum sea level rise to affect the Welsh Basin and predating the FAD of *persculptus* biozone graptolites in Wales, imply a late Hirnantian (upper *extraordinarius* biozone) age. However, the upper boundary of the *Spinachitina* cf. *taugourdeaui* biozone is currently poorly constrained in Wales. Here the upper Hirnantian Baltoscandian *C. scabra* biozone is not recognised and the anticipated lowermost Silurian *fragilis* and *postrobusta* biozones of Verniers et al. (1995) remain unproven below a succession of younger Llandovery and Wenlock biozones (Verniers, 1999; Davies et al., 2013). The same cautionary comments apply here as for the *B.* cf. *gamachiana* biozone, but the implications of better preserved and positively identified specimens of *S. taugourdeaui* found elsewhere in the Welsh Basin are assessed below.

8. Regional correlation and interpretation

The six mid-Katian to Hirnantian chitinozoan biozones recognised in this study permit the more precise correlation of the succession developed in the west of the Welsh Basin, as seen along the Cardigan Bay coast, with that present in the east of the basin and along its marginal shelf (Tywi Anticline, Garth and Llandovery areas) (Fig. 10).

In the Cardigan Bay area, the index taxon for the *Saharochitina spinifera* biozone as well as the taxa normally associated with this middle Katian chitinozoan biozone are absent from the strata sampled as part of this study. Whereas the possible presence of *T. bergstroemi* at Frongoch (Vandenbroucke et al., 2008b) and its certain occurrence at Gwbert implies that the *bergstroemi* biozone may indeed extend downwards from Nantmel Mudstones Formation into the underlying Cwm Yr Eglwys Mudstone Formation as Vandenbroucke et al. (2008b) suggest. It follows, in accord with Vandenbroucke et al. (2005) and contrary to Fortey et al. (2000; see also Davies et al., 1997, 2003), that the base of the Pusgillian and possibly the Cautleyan may lie well below the base of the Nantmel Mudstones Formation throughout mid Wales. Unfortunately the long ranging chitinozoans obtained from comparable statigraphical levels in the east of the basin (Fig. 9) fail to aid regional correlation.

The FAD of the index taxon for the *S. fossensis* biozone lies below the lowest Red Vein anoxic unit exposed on the Cardigan Bay coast (below LH^0) but its FAD in the east, in the Bryn Nicol Formation type section, occurs above one such anoxic (LH^2). At face value this points either to some form of ecological control, or it implies that the Red Vein anoxic units are diachronous and cannot be correlated across the basin. In addition, *Spinachitina ?bulmani sensu* Achab (1977a), considered a key associated taxon of the *S. fossensis* biozone by Vandenbroucke et al. (2005), enters alongside *S. fossensis* in the west, but is absent from eastern sections; and the distinctive *Hercochitina* aff. *normalis* enters alongside *S. fossensis* in the east, but first appears on the coast in a sample from LH^1. Further sampling of this section of stratigraphy appears necessary before these inconsistencies can be resolved or fully understood.

The chitinozoans present in the lower part of the Cribarth Formation include taxa found in the *S. fossensis* and *B. umbilicata* biozones of the Cardigan Bay section and in the Tywi Anticline Bryn Nicol section such as *Spinachitina coronata* and *Hercochitina* cf. *longi*. Other taxa are recorded for the first time in the Welsh Basin such as *Hercochitina* sp. A *sensu* Vanmeirhaeghe (2006) and *Belonechitina capitata*.

The base of the *Belonechitina* cf. *gamachiana* biozone is marked by the appearance of the index taxon in the upper part of the Cribarth Formation at Glasallt Fawr in the Llandovery area where the trilobite *B.* cf. *robusta* confirms its Rawtheyan age (see above). Along the Cardigan Bay coast the taxon's first appearance in the second Red Vein anoxic (LH^1) is associated with *anceps* Biozone graptolites. These findings clearly show that *Belonechitina* cf. *gamachiana* enters well below the local base of Hirnantian strata.

The base of the newly-defined local *B. llangrannogensis* n. sp. biozone is recorded from the base of the lower Yr Allt Formation in both the Cardigan Bay and eastern sections allowing good correlation and offering confirmation of the early Hirnantian age for this formation

S. taugourdeaui is recorded in the Hirnant Limestone in the historic type area of the UK Hirnantian Stage (Vandenbroucke et al., 2008a). This distinctive formation is widely viewed as deposited during a Hirnatian glacial maximum (e.g. Brenchley and Cullen, 1984). However, all records of *Spinachitina* cf. *taugourdeaui* in the Garth and Llandovery areas (this study; also Davies et al., 2013) are from post-glacial transgressive facies (Garth House Formation) that pre-date the FAD of *persculptus* biozone graptolites in Wales (Davies et al., 2009). Pending either a reinterpretation of the depositional history of Hirnant Limestone, or the discovery of *S. taugourdeaui* from strata acknowledged as transgressive, the possibility exists that the *S. taugourdeaui* Biozone established in Cwm Hirnant pre-dates the *Spinachitina* cf. *taugourdeaui* Biozone of this study. The absence of both *S. taugourdeaui* and *Spinachitina* cf. *taugourdeaui* precludes any chitinozoan-based correlation with the Cardigan Bay area.

9. Correlation outside the Welsh Basin

Recognition of the *T. bergstroemi*, *S. fossensis*, and *B. umbilicata* biozones allow direct correlation with other Avalonian sections in the Cautley District and in Belgium, where, the *T. bergstroemi*, *S. fossensis* and *B. umbilicata* biozones have also been recognised (Vanmeirhaeghe and Verniers, 2004; Vanmeirhaeghe, 2006).

Outside Avalonia, the presence of the *T. bergstroemi* and *B. umbilicata* biozones provide correlation with Baltoscandia whereas the *B.* cf. *gamachiana* and *S.* cf. *taugourdeaui* biozones carry the potential of correlation with Laurentia and Baltoscandia. The *B.* cf. *gamachiana* biozone in Wales may also demonstrate further similarities of the Avalonian chitinozoan composition with that of Laurentia despite Vandenbroucke (2008a) considering a Baltoscandian signature to be dominant. Furthermore, Vandenbroucke (2008a, 2008b) also records *H.* cf. *gamachiana* and *H.* aff. *gamachiana* from British Avalonia in Cwm Hirnant and Rhayader but until unambiguous material is recovered from Anglo-Welsh sections in Avalonia, this suggestion remains open to speculation.

The *C. rugata* biozone has not been identified in the Welsh Basin in the current study, but has been recognised elsewhere in Avalonia, from the Cautley district in northern England (Vandenbroucke et al., 2005) and the Condroz Inlier in Belgium (Vanmeirhaeghe and Verniers, 2004) where it occurs below the *S. fossensis* biozone (Vandenbroucke, 2008a). The failure of the current study to confirm this biozone may reflect the low sampling resolution below the base of the *S. fossensis* Biozone in the Nantmel Mudstones Formation. However, Kaljo et al. (2008) record *B. umbilicata* from the *rugata* biozone from the Kaugatuma core implying correlation of the Welsh Basin *B. umbilicata* biozone with the upper part of the Baltica *C. rugata* biozone.

Hercochitina cf. *longi*, recorded from the Nantmel Mudstones Formation in the *B. umbilicata* biozone in the Cardigan area and from the *S. fossensis* biozone in the Llandovery area provides further support for correlation with the Avalonian *S. fossensis* biozone and with the upper

Katian (upper Rawtheyan) *Hercochitina florentini–Conochitina concava* biozone of North America (Laurentia, Achab et al., 2013). *Hercochitina* cf. *longi* occurs below the first appearance of *B.* cf. *gamachiana* in keeping with the *Herochitina florentini–Conochitina concava* biozone as defined by Achab et al. (2013). *Hercochitina minuta*, recorded in this study in the *fossensis* biozone, is also mentioned as being an associated taxon of the *Tanuchitina anticostiensis* biozone, which underlies the *Hercochitina crickmayi* biozone (Achab, 1977b). Within the *T. anticostensis* biozone, *H. minuta* is succeeded by *Hercochitina normalis*, each taxon defining a subzone. In the Cardigan–Llangrannog region, *H.* cf. *normalis* is reported above *H. minuta* in the *umbilicata* biozone implying that, if the presence of these two taxa does represent a direct correlation with Laurentian zonation scheme, then the *T. anticostiensis and H. florentini–C. concava* zones may represent the correlative equivalents of the *fossensis–umbilicata* zones in Avalonia. The upper Katian (upper Rawtheyan) *A. merga* biozone, reported from Laurentia, Gondwana, and Avalonia, is not recognised in the Welsh Basin but has been recorded from Avalonia in the Cautley District in England (Vandenbroucke, 2008a).

Correlation of the lower Hirnantian within Avalonia and to other palaeocontinents has previously been inhibited by the lack of a consistent discrete range-defining taxon. Vandenbroucke et al. (2008a) and Vandenbroucke and Vanmeirhaeghe (2007) recognised that *Cyathochitina* spp. and *Ancyrochitina* spp. become abundant in the uppermost Ordovician and lower Silurian and demonstrated this from analysis of samples taken from Cerrig Gwinion Quarry. This pattern is also reported from the Llandovery sections in this study (Fig. 9, Table 3), but these taxa are either long-ranging (*Cyathochitina* spp.) or too poorly preserved (*Ancyrochitina* spp.) to be utilised for biostratigraphical purposes. Following his study of the historic type area for the Hirnantian at Cwm Hirnant, Vandenbroucke et al. (2008a) recognised that *Belonchitina* sp. 11 (*Belonchitina llangrannogensis* n. sp. of this account) may prove a worthy regional zone fossil if more assemblages could be recovered from other Hirnantian horizons. This species, commonly in association with *S. taugourdeaui*, was recovered by Vandenbroucke (2008b) and Vandenbroucke et al. (2005) from Hirnantian sections in the Cautley district and the Welsh Basin (Hirnant Limestone) (Vandenbroucke et al., 2008a) and from the Brabant Massif in Belgium (Vanmeirhaeghe, 2006). These studies appear to reinforce a restricted stratigraphical and palaeogeographical range of *B. llangrannogensis* n. sp., which, at the time of writing, is unknown outside Avalonia.

10. Discussion

H. crickmayi was considered to define a biozone in Laurentia until Achab et al. (2013) recognised three new *Hercochitina* species *Hercochitina florentini*, *Hercochitina longi* and *Hercochitina changi* and erected the *Hercochitina florentini–Clathrochitina concinna* biozone defined by the coexistence of the two taxa. Achab et al. (2013) erected the zone as an assemblage zone to circumvent the difficulty in identifying species of *Hercochitina*, especially when they are poorly preserved. The Welsh Basin *Hercochitina* material is poorly preserved and identification of hercochitinids is made here on shape of test, size range and on what ornamentation is present (see Appendix I). This has regrettably necessitated placing several *Hercochitina* taxa in open nomenclature thus reducing the certainty of correlation outside of the study area, for instance correlating the *Belonechitina* cf. *gamachiana* Biozone with the *H. gamachiana* biozone in Laurentia and Baltica. This is unfortunate given that the chronostratigraphic position of the base of the *B. gamachiana* biozone is disputed.

Achab et al. (2011, 2013) infer that the base of the *B. gamachiana* biozone lies within the Hirnantian. Vandenbroucke (2008a) also records *H.* cf. *gamachiana* from the Hirnant Limestone Member of the Foel-y-Ddinas Mudstone Formation in Wales which is unequivocally of Hirnantian age. However, in Baltoscandia Kaljo et al. (2008) and Hints et al. (2004) consider it to lie in the upper Katian Pirgu Stage. In the Cardigan Bay section, *B.* cf. *gamachiana* occurs in Red Vein anoxics LH^1 and LH^3 in association with graptolite assemblages of the Rawtheyan *anceps* biozone (Williams, 2001a, 2001b). Near Llandovery *B.* cf. *gamachiana* is present in the Cribarth Formation alongside the graptolite *O. abbreviatus* and associated with the trilobite *B.* cf. *robusta* (see above); co-occurrences that are again consistent with a pre-Hirnantian, late Katian (late Rawtheyan) age for the local base of the *B.* cf. *gamachiana* biozone. This can be seen either to support a late Katian age for the base of the Laurentian–Baltoscandia *H. gamachiana* biozone (e.g. Nõlvak, 1999; Hints et al., 2004; Kaljo et al., 2008) contrary to Achab et al. (2011, 2013), or, alternatively, to suggest that the FAD of a precursor to the index taxon allows the underlying *S. fossenis* biozone to be subdivided. The latter interpretation implies the coincidence of the Laurentian–Baltoscandia *B. gamachiana* biozone with the Avalonian *B. llangrannogensis* n. sp. biozone here erected. Until further investigations have documented the stratigaphic and taxonomic relationship of *B.* cf. *gamachiana* to *B. gamachiana*, this remains speculative.

Similarly, further study in Wales is needed to assess the taxonomic and stratigraphic relationships between *S. taugourdeaui* (from the Cwm Hirnant section by Vandenbroucke et al., 2008a) and *Spinachitina* cf. *taugourdeaui*, and to assess the possibility of the latter occurring in slightly younger rocks than the former. Nevertheless, pending further sampling and taxonomy, the Welsh Basin is one of the rare areas where we can (realistically) expect to find better preserved specimens of *B.* (cf.) *gamachiana* and *S.* (cf.) *taugourdeaui* to study in sections with graptolite control.

Several taxa appear to occur anomalously high in the Nantmel Mudstones Formation in the Cardigan Bay section, for example *Cyathochitina* cf. *reticulifera* (sample TJC D941) and *Saharochitina* cf. *fungiformis* (samples TJC D941, TJC D957). These out of context taxa are likely to have been reworked from older sediments and this is consistent with the turbiditic origin of the bulk of the Welsh basin succession (Davies et al., 1997, 2003; Schofield et al., 2004). Reworking is potentially more of an issue in the Hirnantian (Paris et al., 2007). In Wales, the deep erosion of sediment during the associated glacioeustatic lowstand is dramatically indicated by the presence of a pronounced unconformity at the base of the Cwm Clyd Sandstone Formation in Crychan Forest (Davies et al., 2009). Three taxa, *Eisenackitina inconspicua*, *Desmochitina juglandiformis* and *Lagenochitina* cf. *ponceti*, are notably out of place in Hirnantian rocks of the Llandovery region and in the Cardigan Bay section *Desmochitina cocca* is also out of stratigraphic context.

11. Conclusions

A regional chitinozoan biozonation scheme has been developed that provides confirmation and allows refinement of the recently constructed Avalonian chitinozoan biozonation scheme of Vandenbroucke (2008a) (Fig. 11). It identifies the Avalonian *T. bergstroemi*, *S. fossensis* and *B. umbilicata* biozones in the middle–upper Katian of the Welsh Basin. The lowest biozone reported in this study is the *T. bergstroemi* biozone. The underlying *F. spinifera* biozone is not identified in the Nantmel Mudstones Formation in either the Cardigan Bay or more eastern sections. This implies, as proposed by Vandenbroucke et al. (2008b), that the base of the Ashgill (mid-Katian) is lower than the lithostratigraphic boundary that marks the onset of basin oxygenation (base Nantmel Mudstones Formation). The *C. rugata* biozone, which elsewhere overlies the *T. bergstroemi* biozone, is not recognised in the Welsh Basin in this study although the index taxon has been identified.

At a higher level in the stratigraphy, the presence of the *B.* cf. *gamachiana* and *S.* cf. *taugourdeaui* biozones implies a link to Laurentian and Baltoscandian chitinozoan provinces. However, the base of the *B.* cf. *gamachiana* biozone within the upper Nantmel Mudstones Formation on the Cardigan Bay coast and at a comparable level (upper Cribarth Formation) in the Llandovery area is associated with late Katian (Rawtheyan) graptolites (*anceps* biozone) and trilobites. Further sampling is recommended to validate the presence and lithostratigraphic position of *B. gamachiana* in the Welsh Basin. A new lower to middle

Hirnantian regional biozone, the *B. llangrannogensis* n. sp. biozone, has been defined and typifies rocks that record the local impact of the coeval glacioeustatic regression. This new biozone enables correlation between other Avalonian sections in the Anglo-Welsh region and in Belgium.

This study has found *Spinachitina* cf. *taugourdeaui* within upper Hirnantian strata deposited during a post-glacial maximum rise in sea level and pre-dating the entry of the *persculptus* biozone graptolites in Wales. These occurrences appear to post-date assemblages with *S. taugourdeaui* recognised in the historic type section for the UK Hirnantian Stage. They point to the need to confirm the sedimentary interpretation of this section and to establish the relationships between *S. taugourdeaui* and *Spinachitina* cf. *taugourdeaui* within the Welsh Basin.

Chitinozoan assemblages have contributed to the improved correlation of the basin centre Cardigan Bay succession with sections in the east that record deposition at the basin margin and on its shelf. This demonstrates the growing effectiveness of Lower Palaeozoic chitinozoan biozonal schemes as correlative tools across a range of palaeogeographical and palaeoecological settings. However, distinct differences in the FADs of some taxa are apparent, notably the index taxa for the *S. fossensis* and *S.* cf. *taugourdeaui* biozones. In implying some palaeoecological constraint on their distribution, this urges caution in the selection of the taxa employed in the erection and definition of the evolving Avalonian chitinozoan biozonal scheme.

Acknowledgements

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Appendix I. Chitinozoan systematics

In the following systematic discussion of the taxa recovered in this study, the chitinozoan classification scheme of Paris et al. (1999) is adopted whereby genera and species are identified on diagnostic characters of vesicle shape and surface ornamentation. The taxa are presented in the same order as Paris et al. (1999) following his suprageneric classification system. The terms used to describe chitinozoan vesicle shape and ornamentation are those proposed by Paris et al. (1999).

All biometric data are given in µm and the following chamber dimensions have been measured on each specimen where preservation permits: following abbreviations in Paris et al. (1999)

L	total chamber length
Dp	maximal diameter
Dc	diameter of the neck at the flexure (if present)
L:Dp	ratio of L to Dp
N	number of chitinozoans used in calculation.

For each metric, the maximum, mean and minimum values are given when N > 3. When N < 3, the metrics are given in decreasing value. Figures given in brackets following a sample number for "Material" or in a plate caption refer to the unique specimen number for that specimen in the sample.

Biometric data for flattened specimens have not been corrected.

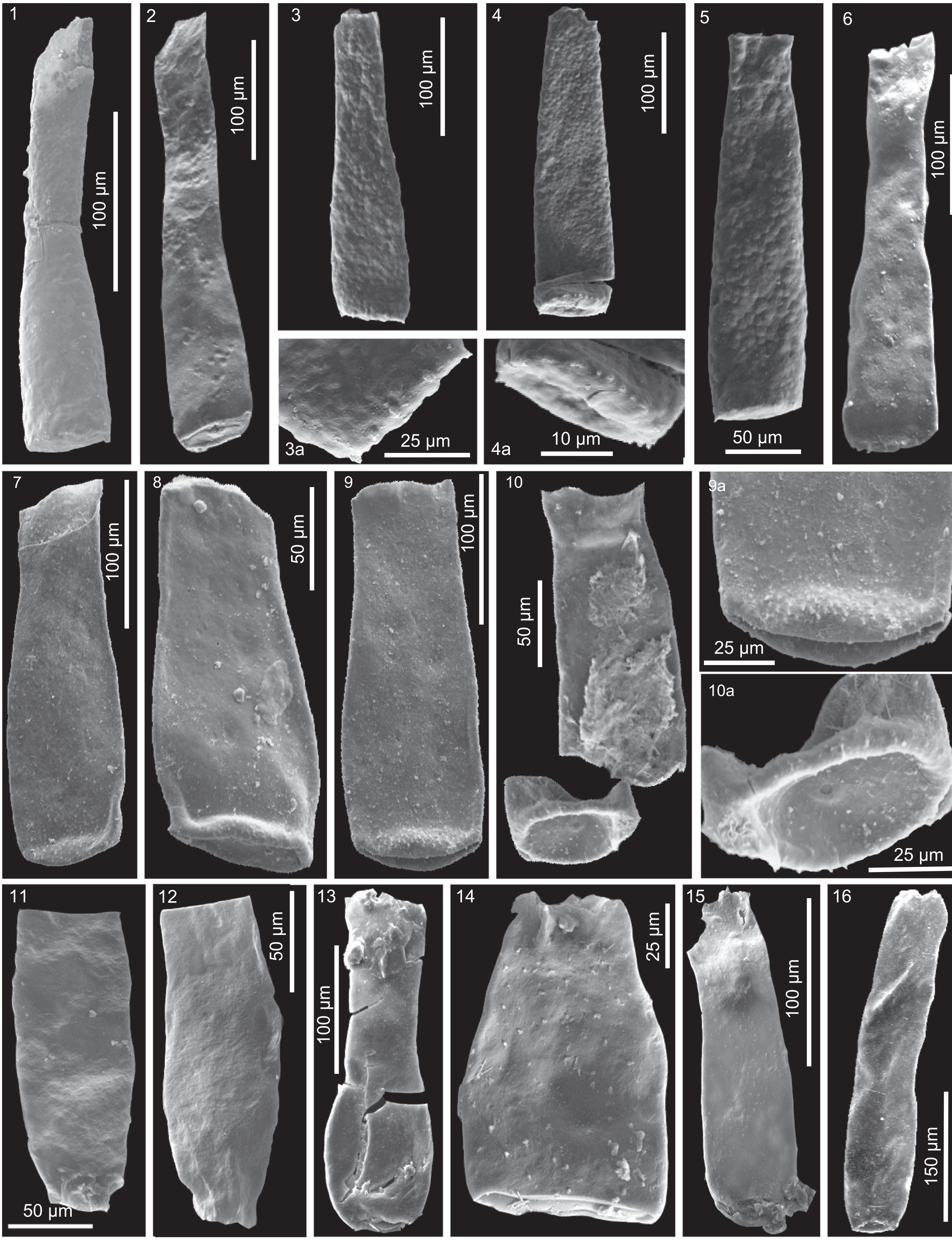
See supplementary information for details of sample number localities.

Incertae sedis group Chitinozoa Eisenack, 1931
Order Prosomatifera Eisenack, 1972
Family Conochitinidae Eisenack, 1931, emend. Paris, 1981 Subfamily Spinachitininae Paris, 1981
Genus *Spinachitina* Schallreuter, 1963 emend. Paris et al. (1999)
Type species: *Conochitina cervicornis* Eisenack, 1931.
Spinachitina penbryniensis Challands, Vandenbroucke, Armstrong et Davies, sp. *nov*.
v.1977a *Conochitina* aff. *bulmani* (Jansonius, 1964); Achab, p.418, pl.2, figs. 1–6, pl.3, figs. 1–3,5,6.
v. 2003 *Spinachitina* cf. *coronta*; Vandenbroucke et al., p.127,. fig. 10 e, f., m
v.2005 *Spinachitina* aff. *bulmani* (Jansonius) *sensu* Achab, 1977a; Vandenbroucke et al., tab. 3, fig. 8.
v.2005 *Spinachitina* ?*bulmani* (Jansonius) *sensu* Achab, 1977a; Vandenbroucke et al., p.789, fig. 12, w [print error in name; same specimens as in record above].
2008b *Spinachitin*a aff. *bulmani sensu* (Jansonius) *sensu* Achab, 1977a; Vandenbroucke, p. 50, pl. 20, figs. 14–16.

Holotype: Plate I, fig. 1 (sample TJC D1013-19, British Geological Survey).
Holotype dimensions: L: 300 µm, Dp: 62 µm, Dc: 39 µm.
Paratype: Plate I, fig. 6. (sample TJC D943-18, British Geological Survey).
Dimensions: L: 366-183-90 µm, Dp: 100-65-45 µm, Dc: 85-44-20 µm, L/Dp: 5.8-2.9-1.5.
Holotype repository: British Geological Survey, Keyworth, UK.
Type stratum: Laminated hemipelagite horizon 1 (LH^1), Nantmel Mudstones Formation, Traeth Penbryn, Ceridigion, Wales.
Etymology: From the hamlet of Penbryn, Ceredigion, Wales, were the type assemblage was recovered.
Material: 94 specimens; 4 specimens from sample TJC D943, Pen-y-Craig, Nantmel Mudstones Formation; 34 specimens from samples TJC D1013-1014, LH^0, 240 cm on log 1, Aberporth; 21 specimens from sample TJC D1015, LH^0, 340 cm on log 1, Aberporth; 15 specimens from sample TJC D979, LH^1, Traeth Penbryn; 1 specimen from sample TJC D957, LH^2, Traeth Penbryn, 2 specimens from sample TJC D956, LH^3 oxic–anoxic boundary oxic facies, Traeth Penbryn; 11 specimens from sample TJC D1010, LH3, Traeth Penbryn. All samples from the Cardigan region.
Diagnosis: A *Spinachitina* species with a long neck approximately the same length as the claviform vesicle chamber and a chamber base surrounded by short, coniform spines directed ante-aperturewards. *Description*: The chamber base is very slightly convex and the basal edge sharp with a

Plate I.

1–3, 3a, 4, 4a, 5, 6.	*Spinachitina penbryniensis* Challands, Vandenbroucke, Armstrong and Davies n. sp. from laminated hemipelagite 1 (LH^1) anoxic facies and oxic facies between LH^1 and LH^2 (1–5) and Nantmel Mudstones Formation oxic facies, Traeth Penbryn (6). (1) Holotype, TJC D1013-19; (2) TJC D979-117; (3) TJC D979-74; (3a) Detail of spines on basal edge of TJC D979-74; (4) TJC D979-22; (4a) Detail of basal edge of TJC D979-22; (5) TJC D979-53; (6) Paratype, TJC D943-18;
7-9, 9a, 10, 10a.	*Belonechitina ceredigionensis* Challands, Vandenbroucke, Armstrong and Davies n. sp. from the Yr Allt Formation, Llangrannog. (7) TJC D1005-65; (8) TJC D1005-38; (9) Holotype, TJC D1005-20; (9a) Detail of basal edge of holotype showing simple dense simple spines becoming smaller up vesicle; (10) TJC D1005-1; (10a) Detail of base of TJC D1005-1 showing simple spines and mucron structure.
11-12.	*Laufeldochitina* sp. Paris, 1981. From the Yr Allt Formation, Traeth Yr Yscland. (11) TJC D946-19; (12) TJC D946-19.
13.	*Lagenochitina* cf. *ponceti* Rauscher, 1973. From the Garth House Formation, Garth House. TJC D976-45.
14.	*Belonechitina* sp. Eisenack, 1959. From the Yr Allt Formation, Traeth Yr Yscland. TJC D946-31.
15.	*Belonchitina* sp. 12 *sensu* Vandenbroucke, 2008b. From the Yr Allt Formation, Traeth Yr Yscland. TJC D946-22.
16.	*Tanuchitina bergstroemi* Laufeld, 1967. From the Nantmel Mudstones Formation, burrow-mottled mudstone oxic facies. Pen-y-Graig. TJC D942-8.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crown of short simple, coniform spines up to 4 μm pointing anti-aperturewards. The number of spines is variable ranging between 5 and 13 as seen on one half of the base of the test. The neck is thinnest at the flexure which is inconspicuous and the width of the neck at the aperture (Dc) is 66–75% the width of the base. The neck wall thins towards the aperture and in the best preserved specimens, flares outwards. The vesicle surface is smooth.
Comparison: This form differs considerably from *S. bulmani* in being almost three times longer; the length of *S. bulmani* being between 100–200 μm (Jansonius, 1964). Also, *S. bulmani* may possess multipode spines whereas those of *S. penbryniensis* are distinctly coniform. It does not have the distinct flexure towards the base of the vesicle that *S. coronata* possesses and the conical shape of the chamber is less well defined and maximum L/Dp is greater than *S. coronata* (=4.2). *Spinachitina kourneidaensis* does not possess a claviform vesicle chamber and has a greater maximum thickness than *S. penbryniensis* (70–130 μm and 45–100 μm respectively). *S. penbryniensis* also lacks the fine tubercular vesicle surface texture of *S. kourneidaensis.*
Remarks: The long, thin fragile neck is frequently broken off specimens but it is still recognisable from the claviform chamber and short, downward-pointing spines e.g. Plate I, 3 and I, 4. Where the number of spines around the base of the test is high, the presence of these being the bases of bi-rooted spines cannot be ruled out.

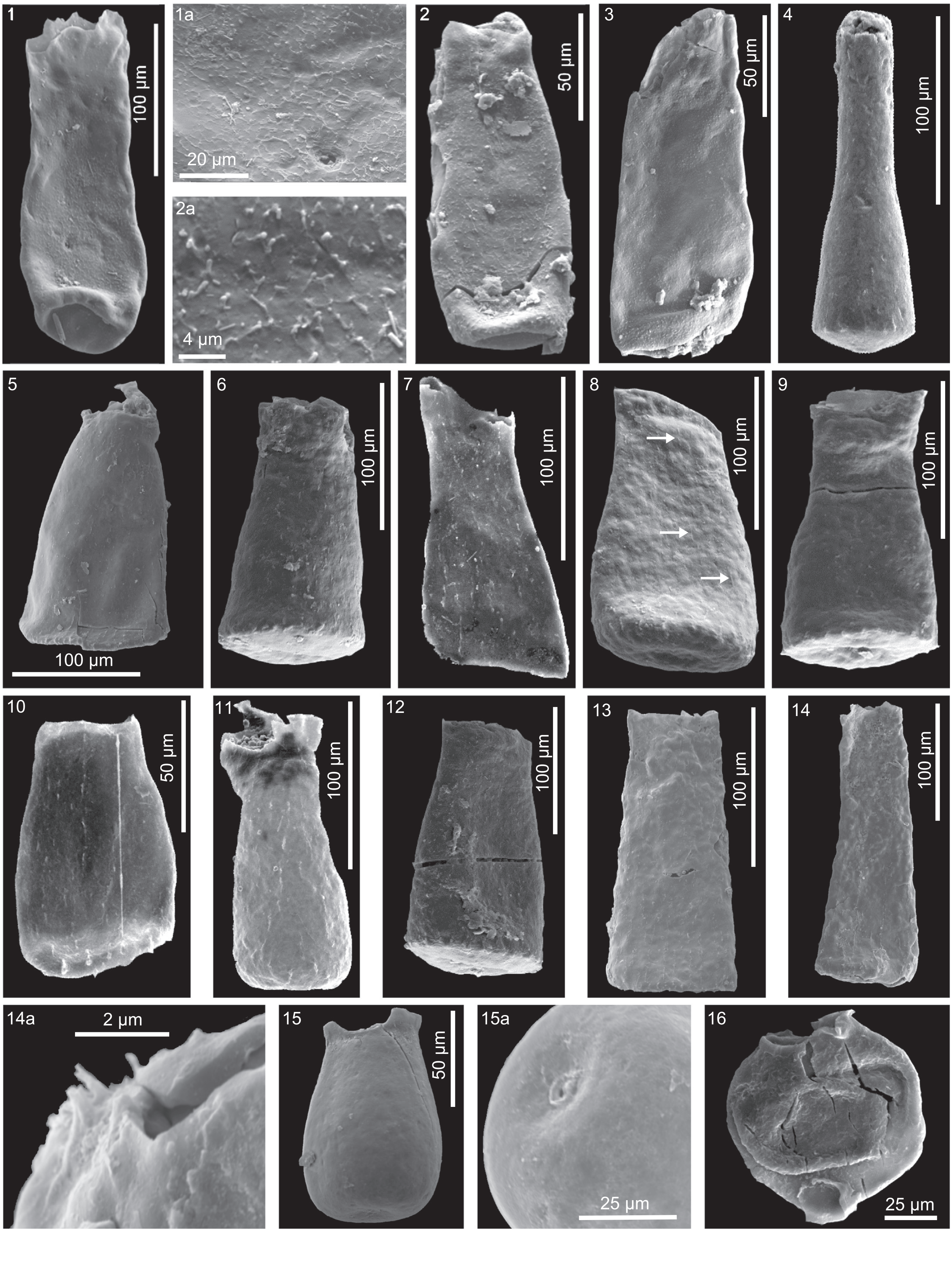
Subfamily Belonechitinae Paris, 1981
Genus *Belonechitina* Jansonius, 1964
Diagnosis: Conochitinidae with a conical chamber and randomly distributed spines.
Belonechitina ceredigionensis Challands, Vandenbroucke, Armstrong et Davies, sp. *nov.*
v. 2008b *Belonchitina* aff. *brittanica*; Vandenbroucke, p. 35–36, pl. 2, fig. 10
Holotype: Plate I, fig. 7 (sample TJC D1005-20, British Geological Survey).
Holotype dimensions: L: 250 μm, Dp: 90 μm, Dc: 70 μm, L/Dp: 2.8.
Holotype repository: British Geological Survey, Keyworth, UK.
Type stratum: Yr Allt Formation, Traeth Penbryn, Near Penbryn, Ceredigion, Wales, UK.
Etymology: From the Welsh county, and former kingdom, of Ceredigion, west Wales, UK, from where the type assemblage was recovered.
Material: 44 specimens: 41 specimens from sample TJC-D1005, Lower Yr Allt Formation, Traeth Penbryn; 3 specimens from sample TJC D1015, Nantmel Mudstones Formation, LH^0, Aberporth,.
Dimensions: Traeth Penbryn: L: 280-212-120 μm, Dp: 100-85-60 μm, Dc: 85-64-30 μm, L/Dp: 3.9, 2.5-1.5; Aberporth: L: 175-165-155 μm, Dp: 70-60-50 μm, Dc: 45-38-35 μm, L/Dp: 3.1-2.8-2.4;
Diagnosis: A species of *Belonechitina* with a claviform test and slightly ovoid chamber with maximum thickness at half the chamber length. The test is ornamented with simple coniform and λ-shaped spines that are larger and denser around the basal margin.
Description: The chamber has a rounded basal margin and a concave base bearing a basal scar c. 5 μm in diameter. The neck is conical with a weak flexure. The distribution of spines is generally sparse, except around the base, and decreases in density aperturewards. A circular mucron-like structure may be present in the centre of the base.
Comparison: This species has a more ovoid chamber and is considerably larger than *Belonechitina brittanica* (L: 150 μm, Dp: 60 μm, Dc: 45 μm). Some of the simple coniform spines may in fact be broken λ-shaped spines. *B. robusta* and *Belonechitina chydea* both have a more conical chamber and the latter does not possess λ-shaped spines. This species differs from *Belonechitina capitata* and *Belonechitina micracantha* in lacking a constriction around the base and a more even covering of spines.

Belonechitina llangrannogensis Challands, Vandenbroucke, Armstrong et Davies, *sp. nov.*
v. 2005a Belonechitina sp. 6; Vandenbroucke et al., tabs 1, 3.
v. 2005 Belonechitina sp.11; Vandenbroucke, p. 172, pl. 26, figs. 6, 15; pl. 30, figs. 1, 2; pl. 31, figs. 1, 10.
2007a Belonechitina sp.11 *sensu* Vandenbroucke (2005); Vanmeirhaeghe, pl.27, figs. 13, 14, 16.
v. 2008a Belonechitina sp.11; Vandenbroucke et al., tables 1–3, figs. 3, 5.
v. 2008b Belonechitina sp.11; Vandenbroucke, p. 46, pl. 21, figs. 6, 15; pl. 26, figs. 1, 2; pl. 27, figs. 1, 10; pl. 29, figs. 1, 2

Holotype: Plate II, fig. 2 sample TJC D946-45 (British Geological Survey).
Holotype dimensions: L: 138 μm, Dp: 64 μm, Dc: 42 μm, L/Dp: 2.16.
Holotype repository: British Geological Survey, Keyworth, UK.
Type stratum: Yr Allt Formation, Taeth Yr Yscland, near Llangrannog, Ceredigion, west Wales, UK.
Etymology: From the small hamlet of Llangrannog, Ceredigion, Wales, UK.
Material: 21 specimens; 15 specimens from sample TJC-D1005, Lower Yr Allt Formation, Traeth Penbryn; 4 specimens from sample TJC D946, Yr Allt Formation, Llangrannog, Cardigan region; 1 specimen from sample TJC D976, Garth House Formation, Garth Bank, Llandovery region; 1 specimen from sample TJC D980, Yr Allt Formation, Dolaucothi M8 core.
Dimensions: D1005, Yr Allt Formation, Traeth Penbryn: L: 285-202-150 μm, Dp: 120-96-80 μm, Dc: 90-67-50 μm, L/Dp: 2.4-2.1-1.9.(N = 15) D946 Yr Allt Formation, Llangrannog: L: 170-160-145 μm, Dp: 80-70-60 μm, Dc: 55-45-40 μm; Yr Allt Formation, Dolaucothi M8 core: L: 187 μm, Dp: 54 μm, Dc: 52 μm.
Diagnosis: A *Belonechitina* species with a claviform to steeply conical chamber and a short cylindrical neck. The vesicle wall entirely is covered by densely distributed thin cones or very small spines, which may be bi-rooted and interlinking, giving characteristic a delicate mesh-like appearance.
Description: The base is flat and the basal margin is rounded. The neck is conical with a weak flexure.

Plate II.

1, 1a, 2, 2a, 3.	*Belonechitina llangrannogensis* Challands, Vandenbroucke, Armstrong and Davies n. sp. from the Yr Allt Formation, Traeth Yr Yscland. (1) TJC D946-12; (1a) Detail of surface of TJC D946-12 showing 'lacy mesh-work' texture; (2) Holotype, TJC D946-45; (2a) Detail of surface texture of TJC D946-45; (3) TJC D946-29.
4.	*Hercochitina* sp. 1 *sensu* Vanmeirhaeghe, 2006. TJC D967-1. From the Nantmel Mudstones Formation, laminated hemipelagite unit 1 (LH^1), Traeth Penbryn.
5.	*Hercochitina* sp. TJC D1013-22. From the Nantmel Mudstones Formation, laminated hemipelagite unit 0 (LH^0), Pen Traeth Bach.
6.	*Hercochitina* aff. *normalis* Achab, 1977b. TJC D979-18. From the Nantmel Mudstones Formation, laminated hemipelagite unit 1 (LH^1), Tresaith.
7.	*Hercochitina* cf. *normalis* Achab, 1977b. TJC D955-7. From the Nantmel Mudstones Formation, laminated hemipelagite unit 1 (LH^1), Traeth Penbryn.
8.	*Hercochitina* aff. *seriespinosa* Jenkins, 1969. TJC D979-21. From the Nantmel Mudstones Formation, laminated hemipelagite unit 1 (LH^1), Tresaith. Vertical ridges indicated by arrows.
9.	*Spinachitia fossensis* Vanmeirhaeghe and Verniers, 2004. TJC D979-85. From the Nantmel Mudstones Formation, laminated hemipelagite unit 1 (LH^1), Tresaith.
10.	*Hercochitina*? *minuta* Achab, 1977b. TJC D968-19. From the Nantmel Mudstones Formation oxic facies, Traeth Penbryn.
11.	*Belonechitina* cf. *gamachiana* Achab, 1978. TJC D956-22. From the Nantmel Mudstones Formation, laminated hemipelagite unit 3 (LH^3), Traeth Penbryn.
12.	*Hercochitina* cf. *seriespinosa* Jenkins, 1969. TJC D979-41. From the Nantmel Mudstones Formation, laminated hemipelagite unit 1 (LH^1), Tresaith.
13, 14, 14a.	*Hercochitina* cf. *longi* Achab and Asselin, 2013. (13) TJC D1015-St1-22; (14) TJC D1013-27; (14a) Detail of base of TJC D1013-27. Both from the Nantmel Mudstones Formation, laminated hemipelagite unit 0 (LH^0), Pen Traeth Bach.
15, 15a.	*Bursachitina umbilicata* Vandenbroucke, Rickards and Verniers, 2005. (15) TJC D1013-8; (15a) Detail of umbilicus of TJC D1013-8. From the Nantmel Mudstones Formation, laminated hemipelagite unit 0 (LH^0), Pen Traeth Bach.
16.	*Desmochitina juglandiformis* Laufeld, 1967. TJC D976-213. From the Garth House Formation, Garth House.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Comparison: This *Belonechitina* species differs from *B. robusta* in possessing much smaller interlinked spines rather than isolated, larger λ-shaped spines. The surface ornamentation is similar to that of *Belonechitina punctata* but *B. punctata* is more claviform and has a broadly rounded base. *Euchonoichitina sheridani* posesses a similar reticulate surface ornamentation but is smaller, has an ovoid chamber with a rounded base and is of Darriwilian age.

Appendix II. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.revpalbo.2014.07.001.

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